The impacts of habitat fragmentation of Tsitsikamma fynbos, South Africa, on avian nectarivore presence, abundance, and pollination

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DECLARATION

I hereby declare that this dissertation for the degree of Doctor of Philosophy is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another university or for another qualification.

Work submitted in this thesis is original research performed through the FitzPatrick Institute at the University of Cape Town. I, Daniël Cloete, declare that I conducted the research myself, under normal input from supervisors, and have fully acknowledged where I received assistance with field work, data analysis or interpretation. The presented work has not been submitted to another institution in any form to obtain a degree.

Signature: Signed by candidate Date: 11 August 2023, Plettenberg Bay

A drone taking off adjacent to Nature's Valley, Tsitsikamma, to photograph a fynbos patch to estimate protea density.

ABSTRACT

Habitat loss and fragmentation of natural habitat, and other global change drivers resulting from human expansion and development, are putting ecosystems and biodiversity at risk. The Cape Floristic Region (CFR), confined to South Africa and known for its high biodiversity of especially plants, has been subjected to extensive habitat loss and fragmentation through agriculture and other modifying land uses. Habitat loss and fragmentation have the potential to negatively affect pollination systems. A reduction in flowering abundance can result in lower nectar production and availability. This reduction in reliable food, along with a lack of adequate habitat and nesting resources, can reduce the abundance of pollinators which, in turn, may result in reduced seed-set for the plant species that rely on them. This study considers how selected erica and protea plants and the sunbirds and sugarbird that pollinate them are affected by fynbos habitat fragmentation.

The study was conducted in an area of fragmented Tsitsikamma Plateau Fynbos in the eastern region of the CFR. **In Chapter 2**, I described the study area, reported methods used to choose and delineate the 17 study patches, and derived variables that were used in the analyses in subsequent chapters. I identified an expected fragmentation effect using exploratory analyses that investigated patch-similarity based on patch, fragmentation, and focal plant species variables. Large patches with high protea densities and surrounded by indigenous forest were clustered, while small patches with lower protea densities and surrounded by transformed farmland and alien vegetation were clustered separately.

In **Chapter 3**, I explored how these fragmentation patterns affected bird species richness and nectar-feeding birds in fynbos habitat. Based on repeated bird point-counts at 33 locations in the study patches I showed that the surrounding non-habitat matrix contributed to faster species accumulation that led to higher species richness in small patches. Although habitat fragmentation had little direct impact on general bird species richness, it explained differences in nectarivore abundance among patches. The fynbos endemic Cape Sugarbird (*Promerops cafer*) and Orange-breasted Sunbird (*Anthobaphes violacea*), as well as the Malachite Sunbird (*Nectarinia famosa*), were less likely to be recorded at locations surrounded by reduced fynbos habitat, while the habitat-generalist Amethyst (*Chalcomitra amethystina*), Greater Double-collared (*Cinnyris afer*), and Southern Double-collared Sunbirds (*Cinnyris chalybeus*) show the opposite trend. The negative fragmentation impact shown on fynbos specialist bird species presumably resulted from their reliance on fynbos habitat and their exposure to pressures from the surrounding non-habitat matrix.

In Chapter 4, I investigated if habitat fragmentation influenced nectar loads in selected erica (*Erica discolor* and *E. densifolia*) and protea (*Protea neriifolia* and *P. mundii*) flowers through its effect on the abundance of the bird nectarivores that feed on and pollinate these plants. I also considered seasonal protea flowering, nectar availability and Cape Sugarbird abundance in the study area. Although I did not find a marked fragmentation effect on flower nectar load in small patches, total nectar availability per unit area increased with patch size for proteas but decreased for ericas. Orange-breasted Sunbird abundance showed no relationship with erica nectar availability, while numbers of Southern Double-collared Sunbirds and Cape Sugarbirds increased with erica and protea nectar availability, respectively. The number of protea flowers, the amount of nectar available and the number of Cape Sugarbirds per month all showed a strong positive correlation, peaking from around December-June. These findings show the importance of nectar availability in determining nectarivore bird abundance and how fragmentation can affect it between patches.

In Chapter 5, I investigated if habitat fragmentation affected seed-set for *Erica discolor* and *Protea neriifolia* flowers. I did not find a fragmentation effect on *P. neriifolia* seed-set, which reflected that Cape Sugarbirds managed to frequent all patches in the study. *Erica discolor* had higher seed-set in small patches, which might be explained by high sunbird density, thanks mainly to large numbers of Southern Double-collared Sunbirds that visited from the surrounding non-fynbos matrix. As a result, *E. discolor* seed-set was negatively correlated with Orange-breasted Sunbird abundance because this species was impacted by fragmentation. *Protea neriifolia* seed-set showed no relationship with Cape Sugarbird abundance.

In the summary, **Chapter 6**, I discuss how habitat fragmentation affected the study system, but note how its impact varies among species. I also consider the limitations of the study and make suggestions for future research. Based on my findings, I suggest that conservation and managing authorities should aim to conserve and expand on remaining fynbos habitat by, for example, clearing the surrounding non-habitat matrix of invasive alien vegetation and/or rehabilitation such as erosion control and reseeding.

ACKNOWLEDGEMENTS

Undertaking this PhD has affected my life in more ways than I ever could have imagined. I started off with a certain idea of what it would mean for me and ended up rediscovering myself. There were some really dark times, but with the help and support of my family, friends and supervisors, I've come through on the other side as a stronger and more balanced person and with a project that I'm proud of seeing through, and as a body of work. I thank my wife, Chrissie Cloete, for not giving up on me and for believing in me and giving me the space to find myself again so that I could finish the project. She also gave me two lovely boys who will forever make the PhD period worthwhile just because it allowed me to spend so much time with them during their first years. I also thank my close family and especially my parents and parents-in-law for their unconditional support throughout and for supporting us financially for the last period of my PhD. Without their support, I would not have finished, so I will forever be grateful. Thank you to my close friends: Chrissie Madden, Jurgens Meyer, Jean and Sandy du Plessis, Rob and Nadia Scholtz, Charles Whitcher and my "Bybelstudie in die bos" friends, who all stood by me and supported me through this long journey.

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Table of Contents

Chapter 1: General Introduction

Global threats to biodiversity

The world has entered the Anthropocene (Corlett 2015; Gibbard et al. 2022). Humanity's impact, driven by an ever-expanding global reach, is exceeding the impact of natural geological and environmental forces (Lambin & Meyfroidt 2011; Schneider et al. 2011; Corlett 2015). Conservationists recognise human-triggered population declines and species extinctions, which far exceed background rates, as the planet's sixth 'mass extinction' event (Pimm et al. 1988; Dirzo et al. 2014; Vignieri 2014; Rosenberg et al. 2019; Cowie et al. 2022; Rull 2022). The main environmental change drivers that threaten biodiversity are overexploitation (e.g. logging, hunting and fishing), agriculture (e.g. crop and livestock farming, and plantations), urban development (e.g. housing and industry), alien invasive species (e.g. resulting in both competition and predation), disease (e.g. fungal and viral spread), pollution (e.g. agriculture and domestic waste), system modification (e.g. fire regime change, damming of rivers, etc.) and anthropogenic climate change (leading to storms and flooding) (Maxwell et al. 2016; Sánchez-Bayo & Wyckhuys 2019). Change drivers often work fast and in synergy, resulting in an increased extinction risk to many species (Brook et al. 2008; Sage 2020). For example, multiple change drivers threaten 80% of the species categorised as threatened on the IUCN Red List (Maxwell et al. 2016). Overexploitation and agriculture are the environmental change drivers that affect the largest number of species (Maxwell et al. 2016). Combined with alien invasive species, they are responsible for 75% of global species extinctions since 1500 CE (Bellard et al. 2016; Maxwell et al. 2016). Environmental change drivers are also responsible for significant biodiversity changes and loss in South Africa (Chown 2010), the location for this study. These problems are particularly acute in South Africa, one of 17 global megadiverse countries with three terrestrial biodiversity hotspots (Cape Floristic Region, Succulent Karoo, and Maputaland-Pondoland-Albany), that faces significant threats from human population growth and the most extreme economic inequalities in the world (Myers et al. 2000; Francis & Webster 2019; Hoveka et al. 2020). It is possible to lessen the threats posed by change drivers to biodiversity, but it will require a clear understanding of the drivers, and how they interact and impact the environment (Sage 2020).

Habitat loss as a threat to biodiversity

Despite the increasing threat posed by climate change, ongoing habitat modification and loss remains the most imminent threat to biodiversity globally (Pimm & Raven 2000; Sala et al.

2000; Newbold et al. 2015; Maxwell et al. 2016). Humanity is responsible for the loss or transformation of over 50% of natural terrestrial habitats, mainly through agriculture and urban development (McIntyre & Hobbs 1999; Hooke et al. 2012). Historically, fertile areas with rich biodiversity were selected for development and transformation (Anderson et al. 2009). South Africa's development footprint resulted in the same habitat loss and transformation patterns, highlighting the need to adequately assess regional threats to biodiversity (Fairbanks et al. 2000; Biggs et al. 2008). Conservative estimates, that do not capture degradation within natural ecosystems, are that South Africa has lost 22% of its natural habitat since the arrival of European settlers in the 1600s (Skowno et al. 2021). These losses are not distributed uniformly across biomes, with the Fynbos (33% loss), Grassland (41% loss) and Indian Ocean Coastal Belt (66%) biomes impacted the most, primarily through the development of croplands, human settlements and plantations (Skowno et al. 2021).

The Convention on Biological Diversity (CBD) recognised this global threat in 2010 and set biological targets for 2020 to reduce habitat loss, fragmentation, and degradation (CBD 2016). In general, insufficient progress has been made towards these targets globally (Green et al. 2019). Broad society does not generally appreciate the global extent of habitat degradation, loss and fragmentation and how drastically these processes compromise ecological dynamics and ecosystem functioning, or their impact on biodiversity (Haddad et al. 2015; Bradshaw et al. 2021). For example, a global analysis revealed that 70% of forests are within 1 km of areas impacted by humans, and 20% within 100 m (Haddad et al. 2015). Conservation planners and practitioners must prioritise to protect remaining habitat to counter this threat and to build resilience against the looming threat posed by climate change (Foden et al. 2013; Mitchell et al. 2015). A key motivation for this study was my recognition of the threats posed by habitat loss and fragmentation to habitat availability and their implications for conservation.

Aspects of anthropogenic habitat loss and fragmentation

Traditionally, habitat loss and fragmentation were handled as somewhat separate processes (Curtis 1956; Moore 1962). However, researchers soon recognised that these processes are intrinsically and hierarchically linked (Table 1.1, Figure 1.1; Didham et al. 2012). After initial habitat loss, researchers now consider the importance of both the interdependence between the sub-components of fragmentation, and between species responses (Table 1.1; Didham et al. 2012; Le Tortorec et al. 2013). Conservationists need to refine their strategies and management actions to counter the persistent threat posed by anthropogenic habitat loss and fragmentation to biodiversity and ecosystem functioning. To succeed they need to understand the consequences of, the complex pressures brought about by, and the processes and causal mechanisms driving habitat loss and fragmentation patterns (Ewers & Didham 2006; Wilson et al. 2016; Fardila et al. 2017). It is also key to identify and determine how species respond to these factors (Cazetta & Fahrig 2022; Giuntini & Pedruzzi 2023).

Table 1.1: The potential impacts of anthropogenic habitat loss and fragmentation, and potential modifying factors that can interact with the key components.

Component	Aspect	Impact
Habitat loss	*per se*	Anthropogenic-driven habitat loss affects biodiversity directly by reducing species available habitat, and indirectly by increasing their exposure to external factors (Horváth et al. 2019). If you compare initial to later habitat loss, it can lead to a disproportionate increase in extinction by reducing area for habitat specialists, and by introducing hunting/harvesting, disease, and invasive species (Betts et al. 2017).
Habitat fragmentation	Habitat loss interaction	When there are large habitat areas, the effects of fragmentation on biodiversity are typically negligible or can be ascribed to habitat loss (Villard & Metzger 2014; Püttker et al. 2020). Habitat configuration affects biodiversity more with further habitat loss. The relationship is non-linear with increased effects from high, through intermediate and low habitat levels (Hanski 2015; Püttker et al. 2020).
	Patch size and isolation	Both patch size and isolation (distance from other patches) are important for species occupancy in fragmented terrestrial systems (Prugh et al. 2008). Large, connected patches contain more species while small, isolated patches support fewer species with greater extinction risk (Bond 1994; Watson et al. 2004; Prugh et al. 2008; Mitchell et al. 2015). Large areas support larger populations with greater genetic variety and increased ecological mutualisms (Matthysen & Currie 1996; McKernan & Hartvigsen 2001; Harris & Johnson 2004; Loman 2006; Alderman et al. 2011).
	Surrounding non-habitat matrix	Unlike islands, natural patches in terrestrial environments are surrounded by a mosaic of different landscape elements or matrix types (Ewers et al. 2007). Each type affects connectivity and ecosystem service flow between patches differently (Mitchell et al. 2015; Fardila et al. 2017; Matthews 2021), including spatial dynamics of populations, and species occurrence and persistence. Three main mechanisms are involved: enhance or inhibit (e.g. movement for dispersal or pollination); resource availability (e.g. additional resources for patch-dependent species); and the patch edge abiotic environment (e.g. favourable light and wind conditions for patch-dependent species, or disturbances such as fire) (Ricketts 2001; Jules & Shahani 2003; Murphy & Lovett-Doust 2004; D'Antonio et al. 2011; Driscoll et al. 2013; Botzat et al. 2015).
	Shape and edge effect	Organisms that live closer to the edge of a natural habitat patch are more likely to be affected by the different conditions (e.g. water availability, wind conditions, and radiation levels) in the surrounding matrix (Fagan et al. 1999; Püttker et al. 2020). How, and how far into the patch organisms are affected, depends on many factors including matrix composition, patch size and shape, and species-specific characteristics (Fagan et al. 1999; Mitchell et al. 2015).
Modifying factors	Time since fragmentation	Some extinctions (and other effects e.g. change in fire regime) occur soon after fragmentation occurs, but other species extinctions only occur over an extended period (Ewers & Didham 2006; Krauss et al. 2010). Ecologists must account for this 'extinction debt' when assessing the impact of fragmentation (Tilman et al. 1994; Halley et al. 2014; Semper-Pascual et al. 2021). Factors such as competitive or mutualistic interactions, or differing mobility across landscapes determine the rate at which species decline and the order of species loss (Hylander & Ehrlén 2013).
	Study species	The effects of habitat fragmentation should not be over-generalised as it varies with study species (Betts et al. 2014). For example, birds and mammals, both with high metabolic requirements, are particularly sensitive to fragmentation (Prugh et al. 2008). Other traits to consider include the ability to adapt and to move across the matrix, longevity and demographic rates (Driscoll et al. 2013; Villard & Metzger 2014; Haddad et al. 2015).
	Study scale	The study scale (e.g., local or landscape) should be considered when investigating and interpreting the results of a habitat fragmentation study. For example, matrix conditions might only affect the study species after a certain threshold in inter-patch distance is exceeded (Driscoll et al. 2013).
	Study focus	Studies that focus on pattern (e.g. species richness and abundance), more regularly used in habitat fragmentation research because of easier data collection, might have differing conclusions on the effect of fragmentation than studies focusing on process (e.g. population dynamics, biotic interactions, and dispersal)(Fardila et al. 2017).

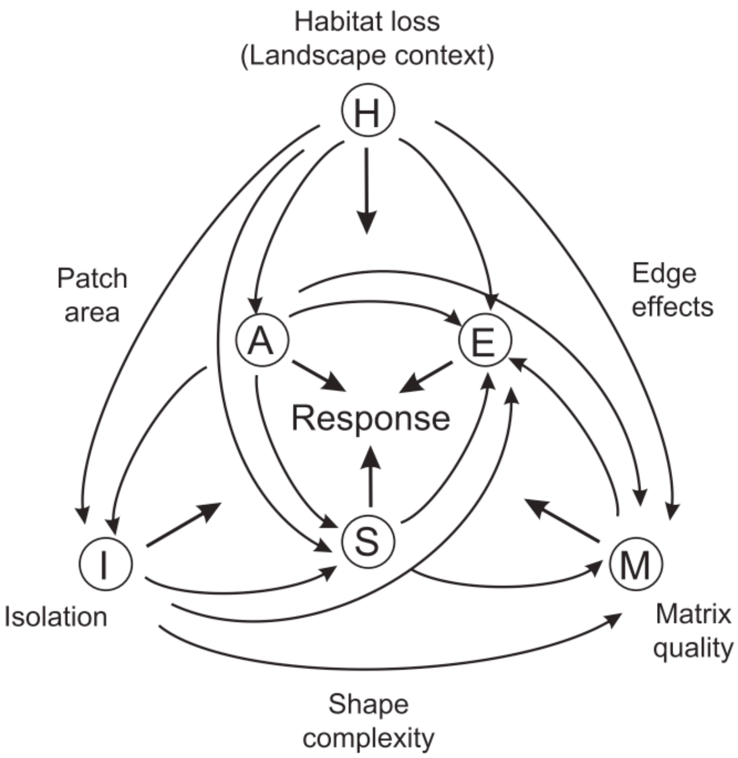


Figure 1.1: Habitat loss and fragmentation occur hierarchically and in an interdependent manner. Initial habitat loss (H) results in the interdependent sub-components of fragmentation: smaller patches of habitat (A) at increased isolation (I), and with more complex shapes (S) and increase edge amount (E), interspersed with the human altered non-habitat inter-patch matrix (M) (Fahrig 2003; adapted from Didham et al. 2012).

Habitat loss and fragmentation research

Researchers initially associated habitat patchiness with spatial heterogeneity and an increase in available habitat (Gause 1934; Huffaker 1958; Fahrig 2017). They considered it to be positive for ecological dynamics at both the level of individual populations and of the community (Den Boer 1968; Levins & Culver 1971; Fahrig 2017). As humanity's influence became more noticeable, we started to associate habitat loss and patchiness with anthropogenic impact and negative population- and community-level responses (Powledge 2003). Since the 2000s, it has been argued that the emphasis should be more on the amount of habitat lost rather than fragmentation per se (Fahrig 2003). This debate is ongoing, with research leading to a new and deeper understanding of the impacts of anthropogenic habitat loss, degradation and fragmentation (Fahrig 2019). In the pursuit of deeper understanding, existing theories are weighed up and newly proposed hypotheses are compared.

Island Biogeography Theory as the foundation

Island Biogeography Theory (IBT) is a seminal concept that underpins ecological science. Developed by MacArthur and Wilson (1967), it shows how island/patch size and isolation determine immigration and extinction rates of species, which determine the equilibrium species richness on an island/patch (Figure 1.2; Wilson 2009). The theory is useful and is broadly applied but has several issues. IBT ignores autoecology i.e. species are not interchangeable, as well as successional effects and the hierarchical links between taxa, and it fails to explain the "small island effect" i.e. species richness varies independent of island size on small islands (Diamond 1975a; Laurance 2008; Araújo & Rozenfeld 2014; Chisholm et al. 2016).

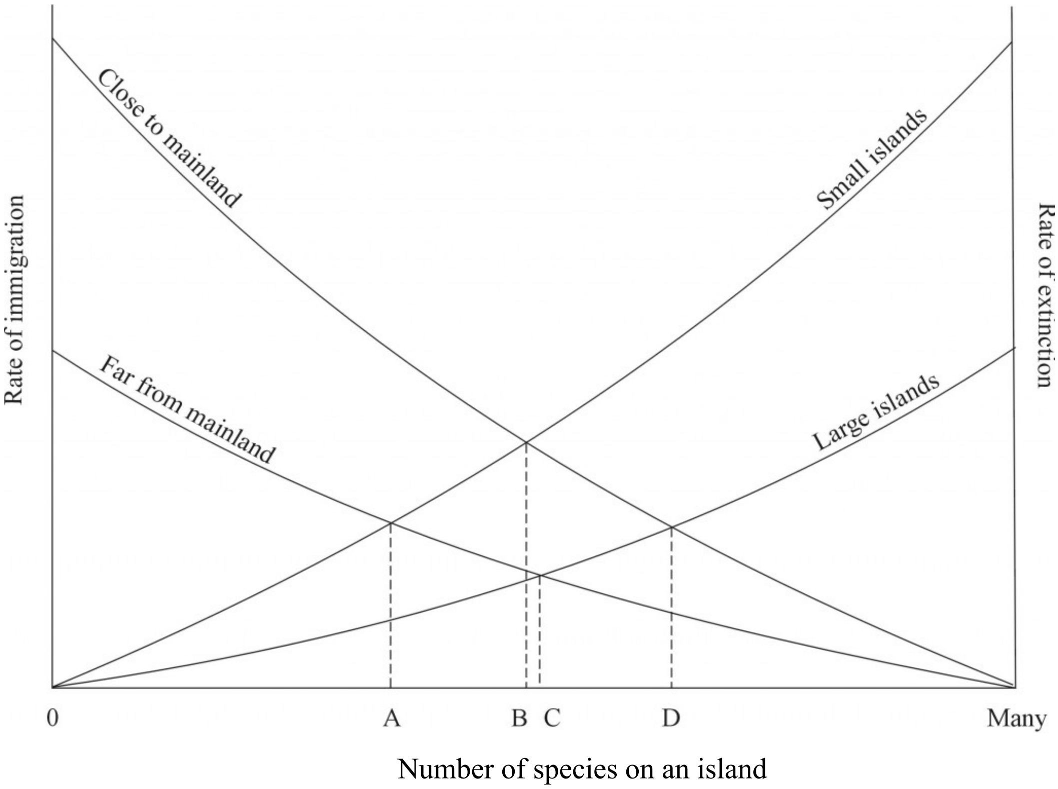


Figure 1.2: Immigration and extinction curves, with the changing intersections of immigration and extinction equilibria predicting the area and distance effects (adapted from MacArthur & Wilson 1967). Small islands far from the mainland (A) will have fewer species at equilibrium than small islands close to the mainland (B).

Levins (1970) first applied IBT to terrestrial patches. Subsequently, Diamond (1975) used IBT in a nature reserve planning guide to suggest that fragmented patches will be detrimental for species conservation. Since then, IBT has been used extensively to argue that anthropogenic habitat fragmentation is a major threat to biodiversity (Laurance 2009). However, it is simplistic to apply a theory developed around a model of natural islands to complex fragmented terrestrial habitat "islands" surrounded by a "sea" of anthropogenic landscapes (Laurance 2008). Ecologists applying IBT to habitat fragmentation research need to consider numerous factors, including; the non-random human conversion of habitat; distinguishing the effects of habitat loss and habitat fragmentation; teasing apart edge and matrix effects and how they interplay with traits that increases a species vulnerability; intra- and inter-species interactions and their effect on species survival and community composition; the altering of ecosystem processes and regimes; interactions of other change drivers that act synergistically on the remaining habitat, and that terrestrial populations and communities are more dynamic

(Laurance 2008; Haddad et al. 2015). Despite these limitations, IBT is a valuable conceptual framework to study and to understand the complex ecological processes in fragmented landscapes (Dondina et al. 2017; Lindgren & Cousins 2017).

Habitat Amount Hypothesis as an alternative

In contrast to IBT, the Habitat Amount Hypothesis (HAH) predicts that the total amount of habitat in the landscape, and not the configuration of patches, determine the slope of species-area relationships (Fahrig 2013). Fahrig (2003, 2013) postulated HAH after finding that habitat loss led to a loss in biodiversity, whereas fragmentation alone (after accounting for habitat area), had a weaker and often positive effect. She also challenged other negative generalisations in fragmentation research, including that large patches contain more species than many small patches; edge effects are negative; fragmentation reduces connectivity; habitat specialist species are especially vulnerable to fragmentation; and that negative effects are strong at low-levels of habitat amounts (Fahrig 2017). Debate on the validity of HAH is ongoing because its predictions for landscape conservation differ from those of IBT. HAH proposes a shift in focus to total habitat area and preventing habitat loss, and a disregard for habitat configuration and connectivity (Haddad et al. 2017; Fletcher et al. 2018).

Present focus in anthropogenic habitat loss research

Considerable research has been conducted to investigate and compare the predictions made between HAH and IBT (Fahrig 2015, 2021; Hanski 2015; Saura 2021a, 2021b). To date, analyses comparing HAH and IBT have found weak negative, neutral, or weak positive effects of fragmentation on biodiversity after controlling for the amount of habitat (Fahrig 2017; Martin 2018). Depending on the species studied and/or the study's specific habitat and surrounding matrix conditions, either HAH or IBT may have more explanatory power and neither will likely be applicable to all situations (Gardiner et al. 2018). For example, IBT may be more suitable for the study of small amounts of remaining habitat in a largely converted landscape (Evju & Sverdrup-Thygeson 2016; Lindgren & Cousins 2017). Some researchers suggest that HAH should be used as a baseline for the effects of habitat loss against which the effects of fragmentation can be contrasted or that both approaches should be applied to complement each other (Martin 2018). These uncertainties suggest that further research is required to understand how habitat loss and fragmentation affect biodiversity. Researchers must consider the specifics and context of their studies so that they can account for the differences and inconsistencies revealed in anthropogenic habitat loss studies (Matthews 2021). They need to understand the implications of assumptions made and also the processes and driving mechanisms responsible for any observed impacts on biodiversity (Table 1.2;

Fletcher et al. 2018; Matthews 2021). Ultimately, research should lead to a better understanding of the threats associated with habitat loss and fragmentation with the aim to effectively manage and conserve impacted species and habitats.

Table 1.2: Key aspects to consider when planning and interpreting habitat loss and fragmentation studies.

Component	Aspects	Consideration
Species	Differences	Habitat loss and fragmentation affect species in different ways depending on their dietary and habitat requirements, and ability to move (Gardiner et al. 2018; Rios et al. 2021). For example, not all species are able to move or disperse over unsuitable habitat between patches.
	Individual or grouped	Fragmentation studies can reach different conclusions depending on whether an individual or a group of species is studied. For example, patterns in species richness of pooled species with different capacities for movement, dispersal, establishment, and persistence reflect processes operating at different habitat amounts and that affect the occurrence of each species differently (Jackson & Fahrig 2012; Hanski 2015; Evju & Sverdrup-Thygeson 2016).
Scale	Local or landscape	Different processes are at work and patterns develop depending on the scale (patch or landscape) of the study. For example, fragmentation on a landscape scale can lead to increased habitat heterogeneity (diversity and number of habitat types) to the benefit of some species (Hanski 2015; Fahrig 2017; Martin 2018).
	Remnant patches	In anthropogenically converted landscapes, habitat patches are not just conceptual. You have to consider and account for distinct remnant habitat patches that are often small and isolated (Hanski 2015).
Mechanisms	Spatial and temporal patterns	Habitat loss and fragmentation processes change over time. We need to understand the underlying change mechanisms to untangle the effect on e.g. species richness, of processes that overlap in space and/or time (Haddad et al. 2015; Evju & Sverdrup-Thygeson 2016).
	Hierarchical system and synergy	There is a strong link between habitat loss and fragmentation, making it difficult to discern their effects independently. The two factors often work in synergy e.g. after a certain threshold of habitat loss (*ca* 70%), negative effects of patch size and isolation become more pronounced and can lead to an increased loss of species (Hanski 2015; Evju & Sverdrup-Thygeson 2016; Haddad et al. 2017; Gardiner et al. 2018).

A global pollination crisis

Pollination is one of the 15 ecosystem services that are in decline because of anthropogenic pressures (Millenium Ecosystem Assessment 2005). Animal pollination, as an important ecosystem service, is a main driver of ecological systems (Carpenter et al. 2009). Animals pollinate an estimated 87.5% of flowering plants (Ollerton et al. 2011). Some authors argue that all other ecosystem services, to a certain extent, rely on pollinators because of their key role in terrestrial ecosystems (Ollerton et al. 2011; Christmann 2019). Ecologists recognise the importance of pollinators for species persistence, biodiversity, and ecosystem integrity (Spira 2001; IPBES 2016; Christmann 2019). Recently pollinator abundance and efficiency has shown a marked decline globally (Powney et al. 2019; Sánchez-Bayo & Wyckhuys 2019). For example, an estimated 16.5% of vertebrate pollinators (30% on islands) are threatened with extinction (Aslan et al. 2013). This has worrying consequences for plant reproduction, and subsequently species loss and possible ecosystem breakdown or collapse (Potts et al. 2010).

The underlying cause of pollinator decline is a complex and synergistic interplay between the natural biological processes of pollinators, and the continuing pressures exerted by global environmental change drivers, including past and present anthropogenic land use and land cover change, climate change, alien invasive spread, disease propagation, and fire and other regime changes (Potts et al. 2010; Vanbergen 2013; Bommarco et al. 2014; Regan et al. 2015; Maxwell et al. 2016).

Habitat loss and fragmentation contributes to the pollination crisis

The impact of habitat loss and fragmentation on pollinators and their ecological role is a concern (Spira 2001; Montero-Castaño & Vilà 2012; IPBES 2016; Sánchez-Bayo & Wyckhuys 2019). Habitat loss and fragmentation severely affect various aspects of pollination and plant reproduction from organismal and population to community level (Aguilar et al. 2006; Xiao et al. 2016). Pollinators are mainly impacted by a reduction in the availability of their food source; reducing the availability of vertebrate nesting sites or insect larval host plants; or by changing the presence, abundance or behaviour of their parasites and predators (Montero-Castaño & Vilà 2012; Vanbergen 2014). These consequences may impact both plant and pollinator community composition (species richness, species abundance, and phenology), which can affect population dynamics (demographic factors, pollination efficiency, nectar and pollen levels and foraging behaviour), and change the relationships between the pollinators and the plants they pollinate (Krauss et al. 2010; Sabatino et al. 2010; Winfree et al. 2011; Hadley & Betts 2012; Scheper et al. 2014; Xiao et al. 2016). Pollination limitation (quantity or quality of pollen) because of a loss of pollinators and/or a reduction in pollinator activities is a key reason for reduced sexual reproductive success (decreased fruit-set, seed and/or seed-set production) in altered and fragmented landscapes (Aguilar et al. 2006, 2019; Anderson et al. 2011; Xiao et al. 2016). A reduction in pollination efficiency is generally more pronounced for smaller and/or more isolated patches (Wilson et al. 2009; Geerts 2011; Mitchell et al. 2015).

Animal pollination has been used to assess the functional state of human-impacted ecosystems (e.g. habitat fragmentation; Garibaldi et al. 2011; Cariveau et al. 2013). The integrity of animal pollination, as a well-studied and understood ecosystem service, can be used as a proxy for the environmental integrity of the whole ecosystem (Dobson et al. 2006; Mitchell et al. 2015). For example, the numerous studies on heliconia-hummingbird systems in South America show how forest loss and fragmentation can cause changes in hummingbird communities and subsequently affect pollination rates and genetic diversity of plant progeny (Bruna & Kress 2002; Hadley et al. 2014; Torres-Vanegas et al. 2021; Jones et al. 2022). A range of factors needs to be considered when attempting to determine the vulnerability of pollinators, as well as the plants they pollinate and the pollinator networks of which they form part, to habitat loss and fragmentation (Xiao et al. 2016). Not all plant species are equally vulnerable to a reduction in pollinators in the short term. This depends on how specialised the plants and pollinators involved are (e.g. generalist or specialist), how reliant the plants are on pollinators for seed-set, and how reliant the plant is on seeds for reproduction (Bond 1994; Astegiano et al. 2015; McCarren et al. 2021). Pollinator species' characteristics also need to be considered, such as how specialised they are to the specific study system (e.g. forest, thicket, or grassland), and their movement capabilities both within and between habitat patches (Prevedello & Vieira 2009; Pauw & Hawkins 2011; Montero-Castaño & Vilà 2012). We need to investigate and understand the underlying causes for the decline in pollinator abundance and pollination efficiency if we are to mitigate the ecological impacts. Research that will inform policy formulation, management decisions and land use practices needs to integrate interdisciplinary perspectives, and should be conducted over various biological and landscape scales (Vanbergen 2013).

The Cape Floristic Region

My study took place in the fynbos vegetation of the eastern Cape Floristic Region (CFR). The CFR, one of only six floristic kingdoms in the world, is restricted to the southwestern tip of Africa, and has one of the richest and most diverse floras globally (Figure 1.3; Manning & Goldblatt 2012). This region harbours more than 9 300 species of vascular plants, of which 68% are endemic to the CFR (Manning & Goldblatt 2012). Due to the high levels of endemism, the CFR is recognised as one of 35 terrestrial global biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2011). Although the mechanisms for this diversity are not fully understood, the high species richness and diversity is partly explained by the diverse ecological gradients in the region and limited dispersal syndromes in many plant groups (e.g. myrmecochory) (Linder 2003; Warren et al. 2011; Manning & Goldblatt 2012; Ellis et al. 2014). Pollination is one of the key components behind the rich floral diversity in the CFR and is represented by insect, bird, wind and mammal pollination systems (Rebelo 1987). Bird pollination is disproportionately important in the CFR with 75% of southern Africa's bird-pollinated plant species, making up almost 4% of the Cape flora, occurring there (Rebelo 1987).

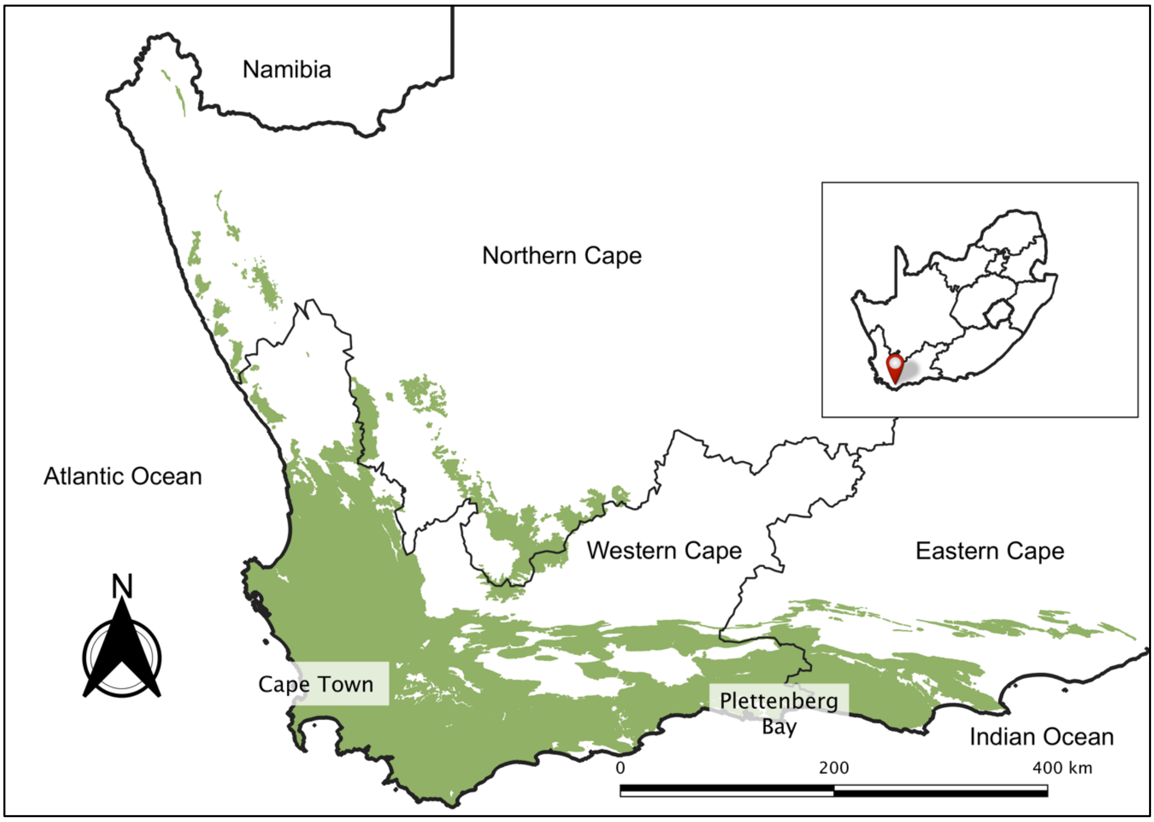


Figure 1.3: The fynbos biome, the main part of the Cape Floristic Region, is restricted mainly to the Western Cape of South Africa (Rebelo et al. 2006).

Habitat loss and other threats to CFR biodiversity

The CFR has lost more than 70% of its original habitat extent (Myers et al. 2000; Mittermeier et al. 2011). The main drivers of habitat loss have been development (mainly along the coast), agriculture and silviculture, inappropriate fire management, and invasion by alien vegetation (Rouget et al. 2003b; Giliomee 2006; Manning & Goldblatt 2012; Kraaij et al. 2013b; Kraaij & van Wilgen 2013). These drivers are still active and it was predicted that a further 30% of the CFR habitat that was remaining in the mid-2000s will be transformed or lost by the mid-2020s if no mitigating actions were undertaken (Rouget et al. 2003b; van Wilgen et al. 2008; Roura-Pascual et al. 2009). Conservative estimates are that an 0.19% rate of loss per year has taken place from 1990 to 2018 (from 71% to 67% of habitat remaining) but that rate has accelerated during recent times with an 0.46% rate of loss per year between 2014 and 2018 (from 69% to 67% remaining; Skowno et al. 2021). Anthropogenic climate change is also predicted to have a negative impact on CFR biodiversity (Midgley et al. 2002; Bellard et al. 2014). Many animals and plants, including endemic fynbos birds, will experience range contractions and shifts, and will be at increased extinction risk (Midgley et al. 2002; Huntley & Barnard 2012; Lee & Barnard 2016).

Fire is the principal driving force in the ecological dynamics of fynbos ecosystems (van Wilgen 2013) and is essential to maintain fire-prone and fire-adapted fynbos (Magadzire et al.

2019). It is likely that the sensitivity of local fauna and flora to fragmentation has been shaped by the natural fire disturbance history of fynbos with potentially only less sensitive species remaining (Betts et al. 2019). In many areas of the CFR, humans have altered the fire regime, mainly for stock grazing. Khoi herders implemented fire management around 1900 years ago, followed by more intense burn cycles by the European settlers from about 300 years ago (Gill 1975; Deacon 1992; Bousman 1998; Neumann et al. 2011). Fynbos managers in the early 20th century considered fire as a destructive force and focused on preventing it (Levyns 1924; Marloth 1924; Pillans 1924; Compton 1926, 1934). A series of seminal studies changed this perspective by illustrating that fire is beneficial and essential for fynbos (van der Merwe 1966; Bands 1977; Boucher 1981; Vogts 1982; Worth & van Wilgen 1988). Subsequently, since around 1968, fynbos managers have practiced ecologically-guided prescribed burning (van Wilgen 2009). However, wildfires (not human-induced burning) mainly determine when fynbos burns (Forsyth & van Wilgen 2008; Kraaij & van Wilgen 2013). For example, wildfires accounted for 80% of fynbos burned in Western Cape protected areas between 1970–2007 (Forsyth & van Wilgen 2007, 2008). Management decisions, complicated by wildfires, may result in shorter or longer than ecologically ideal fire interval windows. For example, some managers may suppress fynbos fires to protect plantations, crops, and inhabited areas, increasing fire intervals, whereas accidental or arson fires may decrease fire intervals (Kraaij et al. 2011; van Wilgen 2013). Such changes to fire regimes can affect fynbos negatively, such as the local extinction of some taxa (e.g. obligate re-seeding long-lived shrubs such as some protea species) if there is insufficient time to recover and produce seed between shortened fire intervals (van Wilgen 1981, 1982; Cowling 1984; Vlok & Yeaton 2000).

Alien invasive plant species have been introduced into the CFR for many purposes, including timber production, dune stabilisation and agriculture (Richardson 1998; Latimer et al. 2004; Kraaij et al. 2011; Baard & Kraaij 2014). *Pinus* (often from commercial plantations) and *Hakea* species spread over mountain catchments, and *Acacia* species spread across lowland areas and along riverbanks (Baard & Kraaij 2014; Rundel et al. 2014; McConnachie et al. 2015). Alien plants impact negatively on CFR biodiversity by displacing and changing species composition, changing soil conditions, increasing water consumption, and increasing fuel loads (van Wilgen & Richardson 1985; Richardson & van Wilgen 2004; van Wilgen et al. 2008; Rundel et al. 2014; Galloway et al. 2017). For example, alien-infested fynbos burns at much higher temperatures, killing seeds and plants that usually germinate and resprout after fire (Brooks et al. 2004; Kraaij et al. 2011, 2013a; van Wilgen 2013). The control of alien invasive vegetation is a major conservation challenge for CFR biodiversity (Mills & Allen 2018). If we fail to control the spread of alien vegetation, the remaining CFR habitat will be further degraded or lost (van Wilgen 2009; Chown 2010).

Study aims, overview and conservation context

Until recently, most fragmentation research was conducted in the Americas and Europe. Other areas, including Africa, are under-represented (Fardila et al. 2017), although some areas in South Africa, such as the western sections of the CFR in Cape Town and surrounds, are better represented (Brown et al. 2011; Pauw & Bond 2011; Heystek et al. 2014). This project adds to the body of existing fragmentation and pollination research globally by studying the impacts of fragmentation in the under-studied eastern sections of the CFR (Rosas-Guerrero et al. 2014; Astegiano et al. 2015; Fardila et al. 2017; SANParks 2017; Millard et al. 2020). The key driving mechanisms involved with habitat loss and fragmentation on pollination systems and plant reproduction are well understood, albeit with many unanswered questions (Xiao et al. 2016). Researchers should avoid making broad generalisations from individual studies. The consequences of habitat fragmentation are dependent on a multitude of factors including the research approach taken (e.g., IBT or HAH), the study scale, the species studied, and the metrics used (Table 1.2). There are no generic solutions to managing fragmented landscapes (Ibáñez et al. 2014; Dondina et al. 2017; Liao et al. 2017). Based on this understanding and coupled with the ever-increasing habitat loss and fragmentation globally, it is imperative to conduct research to understand the mechanisms involved in a specific situation, and how to mitigate the consequences. Therefore, in this study I investigate the impact of habitat loss and fragmentation on fynbos pollinating birds and the plants that they pollinate. I aim to understand the causal relationships identified, and to gain broader insights from the patterns observed (Fischer & Lindenmayer 2007). I weigh up both HAH and IBT theories in my effort to understand the mechanisms through which habitat loss and fragmentation impact nectarivore pollination and fynbos plant reproduction in my study system (Fletcher et al. 2018). My aim is to determine thresholds for the decline and collapse of the plant-pollinator relationships investigated. The thresholds I consider are a range of related factors including smallest patch size and/or connectivity distance between patches, and species composition and abundance of both plants and pollinators.

Policy makers and managers must develop proactive conservation policies and management strategies if we are to stabilise, mitigate, and reverse CFR habitat and biodiversity loss. Practical and targeted research must inform these policies and strategies. I recognised the complicated conservation challenges of the Garden Route National Park (GRNP), the focal area of my study (see Chapter 2 for a description). I planned for my study patches to fall at interfaces between the GRNP, commercial exotic timber/tree plantations, and private land because this is where the remaining fynbos is most threatened and where management guidance is essential. My conservation aim is to contribute scientifically robust spatial data on ecosystem function in the disjointed and fragmented landscape surrounding the GRNP. My findings should inform practical and pragmatic policy and management solutions and guidelines to help safeguard the study area and the broader CFR against present and future threats.

Chapter descriptions

This thesis investigates the impact of habitat loss and fragmentation on selected ericas and proteas and the sunbirds and sugarbirds that pollinate them. In **Chapter 2**, I describe the study area and study sites (including the selection process) and the remote-sensing and GIS methods, and techniques used. This chapter provides in-depth background context for the subsequent chapters. To introduce the fragmentation theme of the study, I use an exploratory analysis to investigate patch similarity based on patch and fragmentation variables and focal protea and erica species density and proportion attributes. In **Chapter 3**, I use repeated bird point-counts to investigate bird species richness and nectarivore abundance in the fragmented fynbos patches of my study area. I test and compare both the effect of local habitat amount surrounding a site and fragmentation configuration on bird populations. I expect that there will be a marked reduction, or even disappearance, of some of the fynbos specialist nectarivore species in the smaller and/or more isolated patches. I also expect that the surrounding non-habitat matrix will have an influence on bird species richness, and that the influence will be more pronounced in smaller patches. In **Chapter 4**, I investigate how nectar availability of selected erica (*Erica discolor* and *E. densifolia*), and protea (*Protea neriifolia* and *P. mundii*) species differ between fynbos patches in fragmented fynbos habitat. I expect that the nectar volumes per flower in different sized patches will depend on how fragmentation factors and the surrounding non-matrix habitat influence bird species variety and abundance, and on the flower species considered. I also test whether nectarivory has an impact on nectar availability. Lastly, I consider monthly flowering phenology of the protea species, and how protea and erica nectar and the respective nectarivores that feed on the flowers relate to each other monthly across the study area. I expect that monthly protea nectar availability will be positively related to protea flower abundance, and in turn, that numbers of Cape Sugarbirds (*Promerops cafer*) will be positively related to both nectar and flower availability. In **Chapter 5**, I investigate if and why the seed-set of *Protea neriifolia* and *Erica discolor* flowers differ between fynbos patches. I consider if these plant species' seed-set is related to the abundance of their respective pollinators (sugarbirds and sunbirds, respectively) in each patch. I expect that *E. discolor* seed-set will be higher in smaller patches because of the introduction of additional suitable pollinators, especially Southern Double-collared Sunbirds (*Cinnyris chalybeus*), from the surrounding non-habitat matrix. For *P. neriifolia*, I don't expect a difference between patches because of the mobility of their main pollinator, the Cape Sugarbird. **Chapter 6** is a synopsis of the findings and conclusions of this study, in the context of the way forward for managing the fragmented fynbos landscape of the greater GRNP region. I also discuss the shortcomings of the study, indicate important avenues for future research, and highlight the conservation and management actions informed by the conclusions of the study.

Chapter 2: Describing the area and fragmentation aspects of a study region in an endangered, fragmented Mediterranean-type ecosystem

Abstract

Humanity's global expansion has as a consequence natural habitat loss and transformation. The study take place in an area of fragmented fynbos habitat in the western Tsitsikamma in the eastern region of the Cape Floristic Region. The study area and methods I define in this chapter serve as the foundation and background for subsequent chapters. I describe the study area in the Tsitsikamma Plateau Fynbos and report how I chose and delineated the study patches. I also describe the fragmentation metrics and focal erica (*Erica discolor* and *E. densifolia*) and protea (*Protea neriifolia* and *P. mundii*) attributes used in the remainder of this thesis and use an exploratory Principal Components Analysis to introduce the fragmentation theme of the study. I assess patch-similarity based on patch and fragmentation variables and composition and abundance of focal protea and erica species. The results show an expected pattern for a fragmented landscape with two distinct clusters found; larger patches with more intact fynbos and natural surroundings i.e. high protea densities surrounded by an indigenous forest matrix, and smaller patches with more impacted fynbos i.e., lower protea densities surrounded by transformed farmland and alien vegetation matrices. In the rest of the thesis, I explore how these fragmentation patterns affect the distribution and abundance of sunbirds and sugarbirds as well as the selected ericas and proteas they pollinate. I explore the drivers behind the patterns found to understand the mechanisms at play and to make practical suggestions for conservation management.

Introduction

A consequence of the global human population's expansion is that natural habitat is being lost and fragmented to fulfil the insatiable need for land and resources (Kerley et al. 2003; Githiru & Lens 2006; Lambin & Meyfroidt 2011). Habitat transformation and fragmentation, identified as a dominant anthropogenic change driver responsible for rapid global biodiversity loss, has been a focus of study since at least the 1950s (Alofs & Fowler 1951; Robbins 1979; Maxwell et al. 2016; Sánchez-Bayo & Wyckhuys 2019). At the heart of such research are questions aimed at establishing effective strategies for conserving biodiversity in fragmented landscapes (Resasco et al. 2017). The core concepts of the impact of fragmentation on species and communities are well understood (Haddad et al. 2015; Xiao et al. 2016; Fahrig 2019), and revolve around the interdependent driving mechanisms of patch size, configuration and isolation on species movement and occupancy, and the impact of the surrounding non-habitat matrix (Fahrig 2003; Smith et al. 2009; Didham et al. 2012). There is considerable variation in the conclusions from studies of habitat loss and fragmentation (Liao et al. 2017; Fahrig 2019). Many factors need to be considered, and each habitat type and landscape and the species or ecosystem that is under threat needs to be studied and understood in its unique context (Ibáñez et al. 2014; Fardila et al. 2017).

The Cape Floristic region (CFR), confined to the southwestern parts of South Africa, is geographically by far the smallest of the world's six floral kingdoms (Werger 1978; Manning & Goldblatt 2012). Fragmentation is a major threat to the low-lying regions of the CFR, which are heavily impacted by commercial and intensive agricultural expansion, and alien vegetation infestation (Kemper et al. 2000; Cowling & Pressey 2003; Lombard et al. 2010). Habitat loss and fragmentation research has taken place in the CFR, but it is still relatively under-studied, especially in the eastern sections of the CFR (Fardila et al. 2017; SANParks 2017). This study focuses on the fragmented Tsitsikamma Plateau Fynbos of the eastern CFR. This area was chosen given the recognition that local research is required to devise effective mitigation strategies for the specific landscape and situation (Ibáñez et al. 2014; Dondina et al. 2017; Liao et al. 2017).

This study investigates the impacts of habitat loss and fragmentation on selected ericas and proteas in the study area and the sunbirds and sugarbirds that pollinate them. In this chapter, I describe the study area in the Tsitsikamma Plateau Fynbos on the southern Cape coast, and the methods that I used to choose and delineate my study patches and to derive variables used in subsequent analyses, including fragmentation metrics and focal protea and erica species attributes. To introduce the fragmentation theme of the study, I use an exploratory Principal Components Analysis to investigate patch similarity based on patch and fragmentation variables and focal protea and erica species density and proportion attributes.

Methods

Study location

I conducted the study in the fynbos in and around the Tsitsikamma section of the Garden Route National Park (GRNP), in the eastern sector of the CFR (Figure 2.1). The GRNP is a patchwork of landscapes consisting of natural patches of mostly forest and fynbos, interspersed with human-modified land (SANParks 2020). This patchwork reflects the area's rich natural diversity, shaped by historical fire patterns, but also past and present human impacts and pressures (Geldenhuys 1994; Baard & Kraaij 2014). Historically, reserve planners aimed to conserve vast tracts of natural land. However, this ideal is seldom attainable, particularly in areas with considerable economic value or potential. Humanity's far-reaching development footprint makes it cost-prohibitive or politically near-impossible to acquire contiguous portions of land (Rouget et al. 2003a; Cox & Underwood 2011; Kraaij et al. 2011; Trimble & van Aarde 2014). The GRNP, established in 2009, reflects a modern park configuration that consists of 30 protected areas interspersed by urban areas, farms, exotic tree plantations and roads (Baard & Kraaij 2014). This configuration exposes the GRNP to ecological disturbances and anthropogenic pressures that threaten its long-term ecological integrity (Spear et al. 2013; McConnachie et al. 2015). The disturbances and pressures include alien invasive vegetation spread, changes in fire patterns, and expanding human development with associated impacts such as effluent pollution in river systems, and the harvesting and poaching of animals and plants (Kraaij et al. 2011; Baard & Kraaij 2014; SANParks 2020).

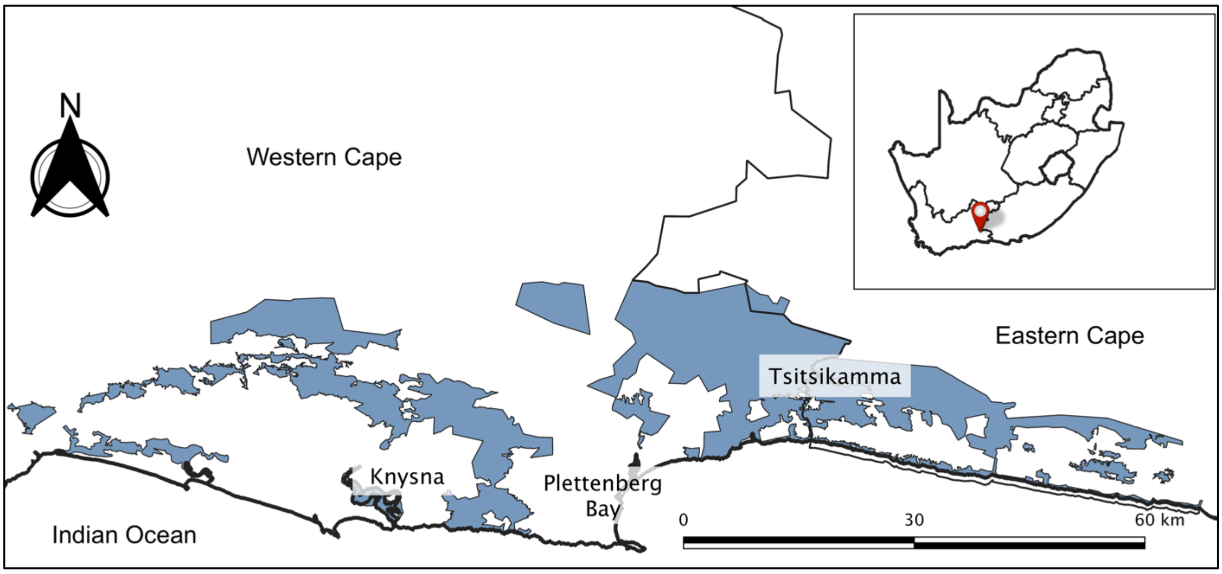


Figure 2.1: The Garden Route National Park, made up of 30 protected fragments (blue) interspersed with human habitats that broadly replaced indigenous habitats.

From the outset, the park management recognised the challenges resulting from the GRNP's configuration. Considering the challenges, a key focus was to balance the GRNP's biodiversity conservation with the socio-economic needs of the surrounding areas. This focus is encapsulated in their management philosophy of "Conservation without Boundaries" (SANParks 2009). In practice this means that management actions are not just focused on the protected area, but also on the equally important stewardship initiatives and other collaborative approaches in adjoining areas. A strategic management goal for the GRNP is to facilitate the conservation of the area's natural heritage by all private land owners and managers (SANParks 2020).

Study area

The study area is located along the southern Cape coast of South Africa, centered on 33.95 °S, 23.53 °E, between Redford in the north and Nature's Valley in the south, and The Crags in the west and Bloukrans in the east (Figure 2.2). The study area was defined based on physical boundaries, with mountainous terrain in the north (requiring specialised transport for access) and the Indian Ocean to the south, and habitat change to the east and the west (Afrotemperate forest and grassy fynbos that lack in proteas).

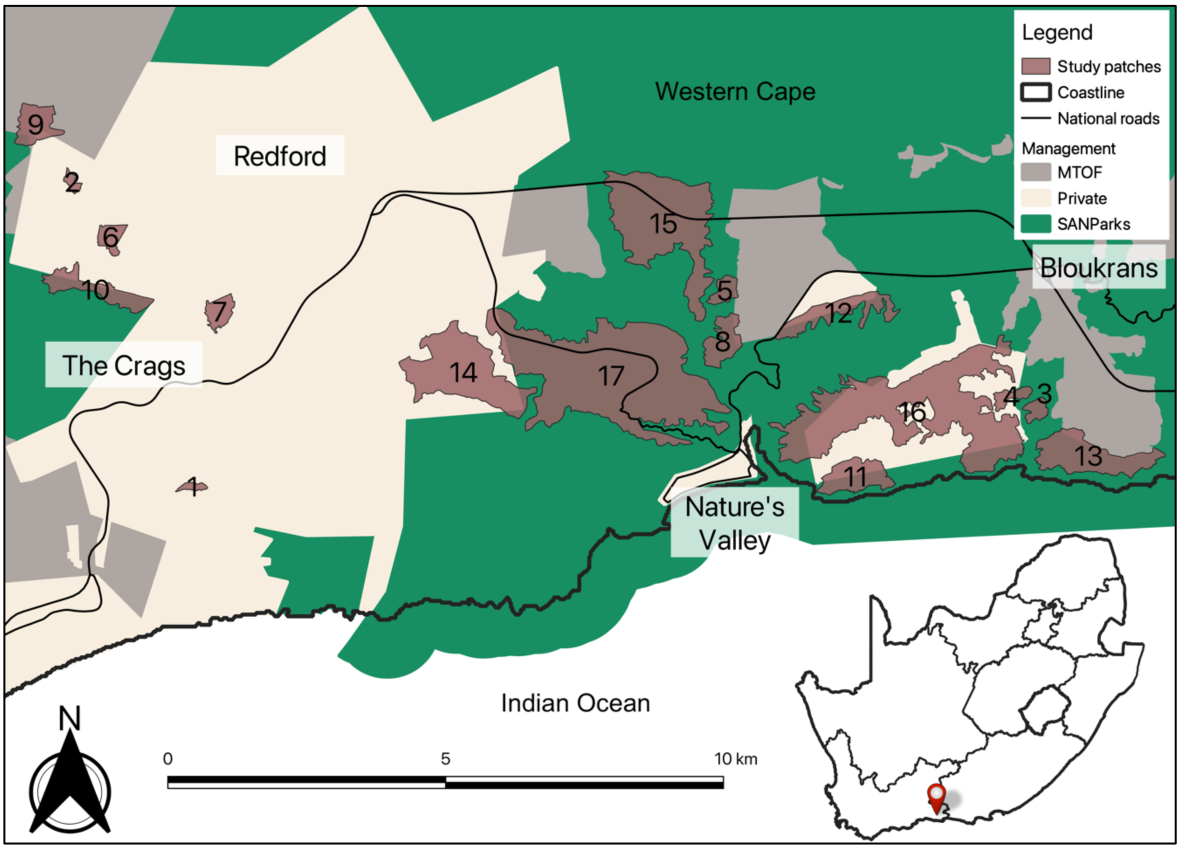


Figure 2.2: The 17 fynbos 'islands' selected as study patches around Nature's Valley on the south coast of South Africa (inset). Fynbos patches are shown in relation to land ownership; Mountain to Ocean Forestry (MTOF), South African National Parks (SANParks) or private.

The southern Cape climate is moderate with warm summers (22–25°C) and mild winters (18–21°C) (Tyson & Preston-White 2000). Katabatic 'berg' winds, which occur regularly in winter, can raise temperatures by up to 10°C to above 30°C (Tyson & Preston-White 2000; Bradshaw & Cowling 2014). Rainfall occurs throughout the year, with peaks in autumn and spring and a drier winter, although prolonged dry spells can occur in both summer and winter (Deacon et al. 1992; Tyson & Preston-White 2000). Annual rainfall ranges from 600 mm at the coast to above 1000 mm in the mountains (SANParks 2020). There is an east-west climatic gradient across the CFR that sees a decrease in seasonality of rainfall, solar radiation, temperature, and evaporation from west to east (Deacon et al. 1992). The Mediterranean climate in the west (cool and wet winters and warm and dry summers) contrasts strongly with the moderate climate (all-year rainfall) in the east, where the study area is located (Tyson & Preston-White 2000; Thuiller et al. 2004; Manning & Goldblatt 2012; Bradshaw & Cowling 2014). This climate gradient affects plant functional traits (e.g. stomatal density, size, shape and area), life history traits (e.g. timing of seed germination, plant recruitment and growth, seed germination, and flowering phenology) and distributions (Johnson 1992; Thuiller et al. 2004; Heelemann et al. 2008; Latimer et al. 2009; Yates et al. 2010; Carlson et al. 2011; Warren et al. 2011; Cowling et al. 2017). These are all factors that I will consider when I compare my results with those from studies conducted in the better-studied western CFR.

The main fynbos vegetation type in the study area is Tsitsikamma Sandstone Fynbos (TSF), which is classified as Vulnerable (Rebelo et al. 2006). TSF is wet fynbos that occurs on both the northern and southern slopes of the Tsitsikamma mountain range (Rebelo et al. 2006) and is a tall, relatively densely growing proteoid shrubland dominated by conebushes *Leucadendron* spp. These shrubs grow over an understory of moderately tall, dense ericoid-leaved shrubs and restios (Rebelo et al. 2006). Plants endemic to TSF include *Aspalathus teres* subsp. *thodei*, *Erica trachysantha*, *E. zitzikammensis*, *Felicia tsitsikamae* and *Helichrysum outeniquense* (Rebelo et al. 2006). Some of the characteristic taller shrubs include *Leucadendron eucalyptifolium*, *Metalasia densa*, *M. trivialis, M. muricata, Protea mundii, P. neriifolia, Laurophyllus capensis* and *Pterocelastrus tricuspidatus*. Lower shrubs include *Erica discolor* var. '*speciosa'*, *E. densifolia, E. sparsa, E. uberiflora, Berzelia intermedia, Euryops munitus, Aspalathus ciliaris, Helichrysum teretifolium, Indigofera flabellate* and *Restio triticeus* (Rebelo et al. 2006). The underlying soils are acidic lithosol derived from Ordovician sandstones of the Table Mountain Group (Rebelo et al. 2006). Southern Afrotemperate forests (a subtype of general Afromontane forest) are found in the wetter habitats in the berg wind shadows east of dissected TSF valleys (Rebelo et al. 2006). The TSF is subdivided into the northern Tsitsikamma Mountain Fynbos and the southern Tsitsikamma Plateau Fynbos (TPF), based mostly on topography and associated plant communities (Pierce 2003). My study area occurs in this latter vegetation type.

The study area falls within the management domain of the Tsitsikamma section of the GRNP, administered by South African National Parks (SANParks), and forms part of the larger Garden Route Biosphere Reserve. The GRNP occurs across a landscape consisting of a natural mosaic of fynbos and forest. This natural mosaic is interspersed by land-use types comprising of present and former forestry exotic tree plantations (mainly *Pinus pinaster* and *P. radiata*), stands of invasive alien woody vegetation (e.g. various *Pinus* spp, *Acacia* spp and *Eucalyptus* spp) and urban and rural settlements including farmland (Kraaij et al. 2011). Land management of the transformed areas falls under Mountain to Ocean Forestry and private land (Figure 2.2).

Fragmentation of natural habitats in the study area through afforestation, cultivation and development has been taking place since the early 1900s, with some fragmented areas isolated from mainland patches for longer than 100 years (Kraaij et al. 2011).

Patch selection

I located potential study patches on large-scale (1:50 000 compared with 1:1 000 000 of Mucina et al. 2014) vegetation maps produced for the Garden Route Initiative (Vlok et al. 2008). All potential patches identified were classified as Montane Mesic Proteoid Fynbos (MMPF) on the vegetation maps and located within TPF (Vlok et al. 2008). The description of MMPF conforms to TPF, being a tall overstory of proteoid shrubs, mostly *Protea* and *Leucadendron*, and abundant ericoid shrubs (Vlok et al. 2008). Of the ten vegetation units classified under MMPF, three overlap with the study area; the relatively tall Tsitsikamma Plateau Proteoid Fynbos, the tall Tsitsikamma Mesic Proteoid Fynbos, and the shorter coastal Covie Coastal Proteoid Fynbos (Vlok et al. 2008). These three vegetation units are comparable for the purposes of the study as they differ only in the local dominance of species and a few localised endemic plant species. Key bird-pollinated species identified for the study are well represented in all three vegetation units (Vlok et al. 2008). The map creators aimed to map the vegetation in its untransformed state prior to European settlement of the region (Vlok et al. 2008). This assisted me in identifying potential patch locations in the highly natural and human fragmented landscape.

I identified some 40 potential fynbos study patches by overlaying satellite imagery with the vegetation maps in both Google Earth Pro 7.3.1.4507 and ArcGIS 10.2.2 (Environmental Systems Research Institute 2014a; Google Incorporated 2018). Google Earth Pro 7.3.1.4507 used satellite-based imagery from a range of national and international sources and 1:10 000 high-resolution aerial imagery was used in ArcGIS 10.2.2 (Environmental Systems Research Institute 2014a; National Geo-spatial Information 2014; Google Incorporated 2018). Both systems provided a complementary perspective for identifying potential patches. I used spatially-referenced data on roads, land use, ownership and management, including erven and farm cadastral data, to identify ownership and management authorities of the potential study patches (National Geo-spatial Information 2014; South African National Parks 2015). I projected all spatial data layers as Transverse Mercator (central meridian = 23.00 °E) in ArcGIS 10.2.2 using the World Geodetic System 1984 coordinate system and Datum (Environmental Systems Research Institute 2014a).

With landowner permission, I visited each potential fynbos patch to determine its suitability for inclusion in the study. Other than being in the historic MMPF area, my selection criteria for suitability were that the patch vegetation consisted of old-growth fynbos dominant vegetation that had never been ploughed or cultivated and that contained *P. neriifolia*. I did not consider fire history as a selection criterion, because the last fire that affected the study area was in 1998, 17 years before my study (Kraaij et al. 2013a). That is nearly double as long ago than the minimum estimated fire return interval of nine years and fynbos nectarivores are most negatively affected in the first five years after fires (Geerts et al. 2012; Kraaij et al. 2013b). Only nineteen patches visited fitted my selection criteria, and I further eliminated two of these as they were overgrown with alien invasive plants (mostly *Pinus pinaster* and *Hakea sericea*). The 17 remaining patches (Figure 2.2; Table 2.1) were mostly clear of alien vegetation, either originally or through recent GRNP eradication programmes (M. Alant, SANParks pers. comm.). I deemed the three largest patches (>200 ha), each also with continuous stands of fynbos, suitable for reference or "pseudo-controls" against which I could compare the smaller patches.

Patch delineation

I delineated a fynbos habitat boundary for each selected patch in Google Earth Pro 7.3.1.4507 and ArcMap 10.2.2 (Environmental Systems Research Institute 2014a; Google Incorporated 2018). I estimated the boundary positions by studying the remote sensed data and from information gained during patch visits. Deep and wide gorges, a prominent feature in the study area, were identified as patch delineators (following St. Clair 2003). For example, the Bobbejaans River and Groot River bridges, on either side of Patch 15 (Figure 2.1), have heights of 175 and 172 m and spans of 165 and 189 m, respectively (Sakowski 2009). These gorges act as barriers to flora and terrestrial fauna movement and dispersion (St. Clair 2003).

Table 2.1: Spatial and surrounding matrix metrics of the 17 patches (arranged by size). Distance between patches is measured edge to edge.

Patch	Size (ha)	Size category	Perimeter (km)	Distance to nearest (km)		Surrounding matrix (percentage of perimeter)			
				Other patch	Large patch	Physical barrier	Alien vegetation	Indigenous forest	Farmland
1	5.7	Small	1.3	2.7	5.78	0	0	100	0
2	6.8	Small	1.4	0.6	7.66	0	51.5	0	48.5
3	13.3	Small	1.9	0.09	0.13	61.8	15.1	23.1	0
4	14	Small	2.3	0.03	0.03	70.1	0	29.9	0
5	17.9	Small	2	0.05	0.05	68.8	23.1	8.2	0
6	18.3	Small	2.2	0.47	6.67	0	48	0	52
7	22.4	Small	2.5	0.93	4.54	0	47.7	0	52.3
8	41.4	Medium	3.9	0.2	0.2	64.5	18	17.4	0
9	42	Medium	3.3	0.6	8.28	0	66.1	0	33.9
10	52.9	Medium	5.8	0.47	6.0	0	27	33.6	39.4
11	58	Medium	4.2	0.22	0.22	48.1	0	51.9	0
12	63.1	Medium	8.2	0.6	0.87	0	4.3	74.6	21.1
13	105.3	Medium	6.7	0.21	0.21	74.8	25.2	0	0
14	190.7	Medium	8.5	0.07	0.07	40.7	25.3	26	8
15	272.3	Large	11.9	0.05	0.38	71.6	0	28.5	0
16	444.1	Large	28.5	0.03	0.69	15.8	0	75.4	8.8
17	565.3	Large	19.8	0.07	0.38	36.1	0	63.9	0

I then used high-resolution images to more precisely define patch boundaries in QGIS 3.1 (QGIS Development Team 2018). The images were acquired with camera-equipped drones, following flight paths planned in Google Earth Pro. Within the restriction of national aviation regulations, including a maximum of 500 m flight radius, and pilot accessibility, I set out the minimum number of flights for each patch to ensure maximum coverage. Images for patches 1, 2, 5, 8, 9 and 12 (Figure 2.2) were photographed on 8–9 May 2017 using a DJI Inspire Pro X5 drone equipped with a 16-megapixel, Micro 4/3 sensor camera. The remaining images (patches 3, 4, 6, 7, 10, 11 and 13–17; Figure 2.2) were photographed on 30–31 May and 5–6 June 2017 by UAV Industries with a DJI Phantom 4 drone equipped with a 12-megapixel, 1/2.3-inch sensor camera. Only sections of some of the patches were photographed because of limited accessibility and time limitations (see Table 2.2 for percentage covered of each patch). Images were taken from a height of 100 m above the launch area. For drone safety and to ensure that images are comparable, all flights were flown during bright daylight and calm wind conditions. I stitched the individual images for each patch into a single composite orthomosaic image using AgiSoft PhotoScan Professional 1.4 (AgiSoft LLC 2018). I used default settings except for the "calibrate colors (with white balance)" setting used between each step to enhance contrast differentiation between light and shadow areas.

Table 2.2: Protea count and density (per ha) for each composite orthomosaic image (COI) and per patch. Patches with incomplete coverage have multiple orthomosaic images that corresponds to the flights flown for that patch and that indicate the percentage of the patch captured by each image.

Patch	**Size (ha)**	**COI size (ha)**	**% of patch captured**	**Proteas per COI image**	**Protea density (n·ha^{-1}) per photographed area**	**Protea density (n·ha^{-1})**
1	5,67	5,67	100	200	35,27	35,27
2	6,79	6,79	100	287	42,2	42,2
3	13,29	13,29	100	110	8,27	8,27
4	13,86	13,86	100	586	42,3	42,3
5	17,85	17,85	100	360	20,15	20,15
6	17,03	17,03	100	2 915	171,15	171,15
7	22,33	22,33	100	2 442	109,34	109,34
8	41,43	41,43	100	322	7,77	7,77
9	41,12	41,12	100	2 466	59,98	59,98
10	52,34	52,34	100	14 825	283,24	283,24
11	58	58	100	1 988	34,27	34,27
12	63,05	63,05	100	8 285	131,41	131,41
13	105,08	105,08	100	15 992	152,2	152,2
14	184,75	55,75	30,2	3 698	66,33	78
		18,25	9,9	2 074	113,64	
15	268,67	65,79	24,5	20 038	304,58	304,56
16	440,88	158,5	35,9	112 860	712,23	603,42
		131,3	29,8	62 013	472,16	
17	561,43	55,28	9,9	8 823	159,61	128,84
		51,95	9,3	6 440	123,97	
		156,7	27,9	18 744	119,59	

Patch spatial metrics and variables

Spatial metrics

I derived spatial metrics for the 17 study patches using Patch Analyst 5.2 in ArcMap 10.2.2 (Table 2.1; Rempel et al. 2012; Environmental Systems Research Institute 2014a). The derived metrics are size (total patch area in ha), perimeter (length of patch in km), edge density (ED; length of edge, which here is perimeter for a patch, relative to area in km^{-1}) and mean shape index (MSI; perimeter divided by the square root of area, following Rempel et al. 2012). MSI is a dimensionless index that increases as the shape becomes more irregular. I assigned size categories to each of the 17 patches based on the approximate size bins they fell into. This resulted in seven small (5-22 ha), seven medium (40-190 ha) and three large (270-565 ha) patches (Table 2.1).

To calculate the distance between patches, I used the "proximity – generate near table" tool of ArcGIS Spatial Analyst in ArcMap 10.2.2 (Environmental Systems Research Institute 2014a, 2014b). Default settings were used except for selecting "find only closest feature" otherwise it also calculates the distances between all patches. I calculated two distance measures for each patch: first, the distance from a patch edge to the edge of the closest other patch, and second, to the edge of the closest large patch (Table 2.1).

Surrounding matrix

I identified the habitat matrix types surrounding each patch from the high-resolution images in QGIS 3.1 (Jules & Shahani 2003; QGIS Development Team 2018) and confirmed these categories during patch visits. I identified nine matrix types but combined them into four categories based on functional similarity (following Sandberg 2013): indigenous forest, alien vegetation, farmland and physical barriers. Physical barriers were hard to cross natural barriers such as deep gorges (all with mostly fynbos at the top edge transitioning into indigenous forest until the edge gets too steep), coastline and mountain sections (the latter two with less than 5% and 1% of combined perimeter for all patches, respectively). Alien vegetation included commercial exotic tree plantations, agricultural and other previously disturbed areas heavily infested with alien vegetation, shallow river valleys with alien vegetation, and indigenous vegetation inundated with alien vegetation. Farmland included cultivated land sections and farm homesteads. I based the matrix type I assigned to a section of patch edge on the dominant habitat within 300 m from that edge. Edge length of each matrix type around a patch was measured in QGIS 3.1 (QGIS Development Team 2018) and expressed as the percentage of the perimeter (Table 2.2).

Protea and erica attributes per patch

Protea neriifolia and *E. discolor* were present in all patches while *P. mundii* and *E. densifolia* occurred in most patches, and so were selected as focal study species. All four of these species are predominantly bird pollinated and no mammal pollinated species were available for selection. I made field notes on these species' attributes in the study area during each patch visit (Table 2.3). I estimated density per patch for both focal erica species using the following categories: 0–none found; 1–scarce; 2–locally common; 3–common throughout the patch. Based on my field notes and point-count observations I estimated the proportion that both focal protea species made up of the overall protea composition for the patches where they co-occurred e.g., 30% *P. neriifolia* and 70% *P. mundii*.

Table 2.3: Focal bird-pollinated plant species and their attributes.

Species	**Patches found**	**Flowering phenology**	**On patch distribution**	**Growth density**	**Flowers per plant**
Erica discolor	17	All year	Throughout	Spars	Few
Erica densifolia	10	Dec-Feb	Patches	Dens	Abundant
Protea neriifolia	17	Feb-June	Throughout	Spars	Moderate
Protea mundii	6	Feb-May	Patches	Dens	Abundant

Protea density

I used the drone-captured high-resolution images to count the number of mature protea bushes in each patch. The use of two drones with different cameras, uneven flight heights as patches differed in topography, and different flight start times and climatic conditions e.g., wind strength and cloud cover, precluded the use of an automated counting process. I thus marked and counted the proteas manually in QGIS 3.1 (QGIS Development Team 2018) by dividing each patch into 50 m^2 grid blocks using the grid tool from the MMQGIS Python plugin (Minn 2020). I GPS marked 10 of each of the two focal protea species (where relevant) in each study patch. I used these GPS marked proteas as visual reference points for each patch to guide protea counting. Protea plants were tagged per grid block at a scale of 1:260 (Figure 2.3). At the capture resolution of the images, it was not possible to differentiate between the two protea species. I marked individual plants with a point and clumps with a polygon where individuals could not be differentiated (Figure 2.3). For the flown areas of each patch, I used the "show feature count" function to tally up all the point tagged proteas. The "field calculator" function was used to calculate the area for each polygon of clumped proteas. I used the "basic statistics for fields" function (under vector – analysis tools) to tally up the total polygon area for the flown areas in each patch. As protea plants had some variation in relative size per patch and/or flown area, I measured the area of 10 randomly selected protea plants on each image to calculate an average protea plant area. I divided the total polygon area by the average protea plant area for that image to calculate the number of protea plants in the polygon areas. The total protea count for each patch/flown area image was calculated as the sum of the point tagged and polygon calculated proteas (Table 2.2). I calculated the protea density per patch for patches covered by a single aerial photograph or where the whole patch area was flown in multiple flights by dividing the total protea count by the total patch area (Table 2.2). A weighted protea density (by percentage of patch captured by each photograph) was calculated for the flown areas when only a proportion of a patch was captured (Table 2.2). I use the weighted protea density as the protea density for the whole patch on assumption that the rest of the patch is comparable in composition to the flown areas.

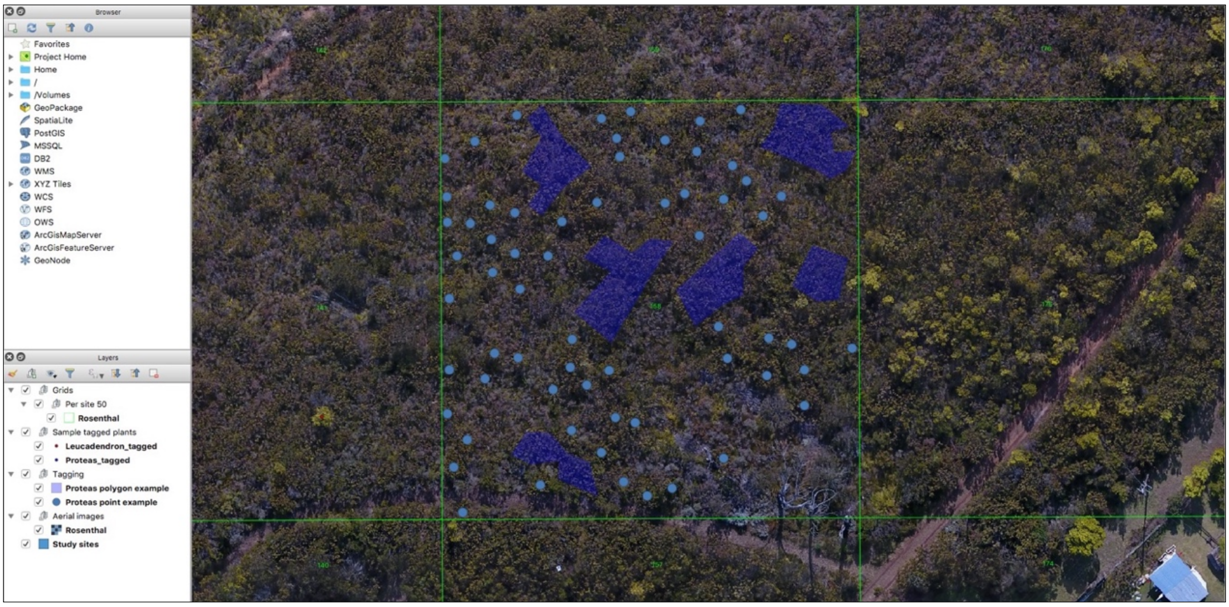


Figure 2.3: Individual protea plants (points) and a protea clumps (polygons) marked in 25 m^2 grids in QGIS 3.1 (QGIS Development Team 2018).

Data analysis

I conducted analyses in R 3.6.1 using the RStudio development framework and the “tidyverse” collection of packages (Wickham et al. 2019; R Core Team 2020; RStudio Team 2022). I calculated correlations between the derived spatial parameters using Pearson's product-moment correlation coefficients with the R function cor.test. Patch size was selected *a priori* as a variable of interest. I discarded parameters that were highly correlated with patch size (all $p < 0.05$). Proportions of *P. mundii* and *P. neriifolia* were strongly negatively correlated with each other. I considered only *P. neriifolia* for further analyses as it occurred in all patches. I used Principal Components Analysis (PCA) ordination to explore patch similarity in terms of patch, surrounding matrix and vegetation covariates described in the methods. I used the R function prcom to produce (centering and scaling the data), and the ggbiplot package to illustrate the PCAs (Vu 2011).

Results

PCA ordination relating descriptive variables to patches

In the PCA relating patch similarity in terms of patch spatial, surrounding matrix and vegetation covariates, the first two PCs explained 56% of the variance, and with PC3 it was increased to 74.7% (Table 2.4). The first two PCs are useful to visualise patch similarity (Figure 2.4).

Table 2.4: The loadings for the first three principle component axes extracted from the patch variables PCA analysis of the Tsitsikamma Plateau Fynbos bird community and the percentage of variation explained by each.

Variables	**PC1**	**PC2**	**PC3**
	(35.5%)	**(21.3%)**	**(17.9%)**
Size	0.39	0.1	0.05
Mean shape index (MSI)	0.39	0.35	0.06
Nearest patch	-0.18	0.28	-0.47
P. neriifolia proportion	-0.3	-0.13	-0.25
Protea density	0.33	0.37	0.24
E. discolor density score	-0.02	-0.14	-0.4
E. densifolia density score	0.29	-0.23	0.22
Physical barriers matrix	0.19	-0.58	0.11
Alien vegetation matrix	-0.4	0.13	0.34
Indigenous forest matrix	0.3	0.22	-0.51
Farmland matrix	-0.31	0.41	0.26

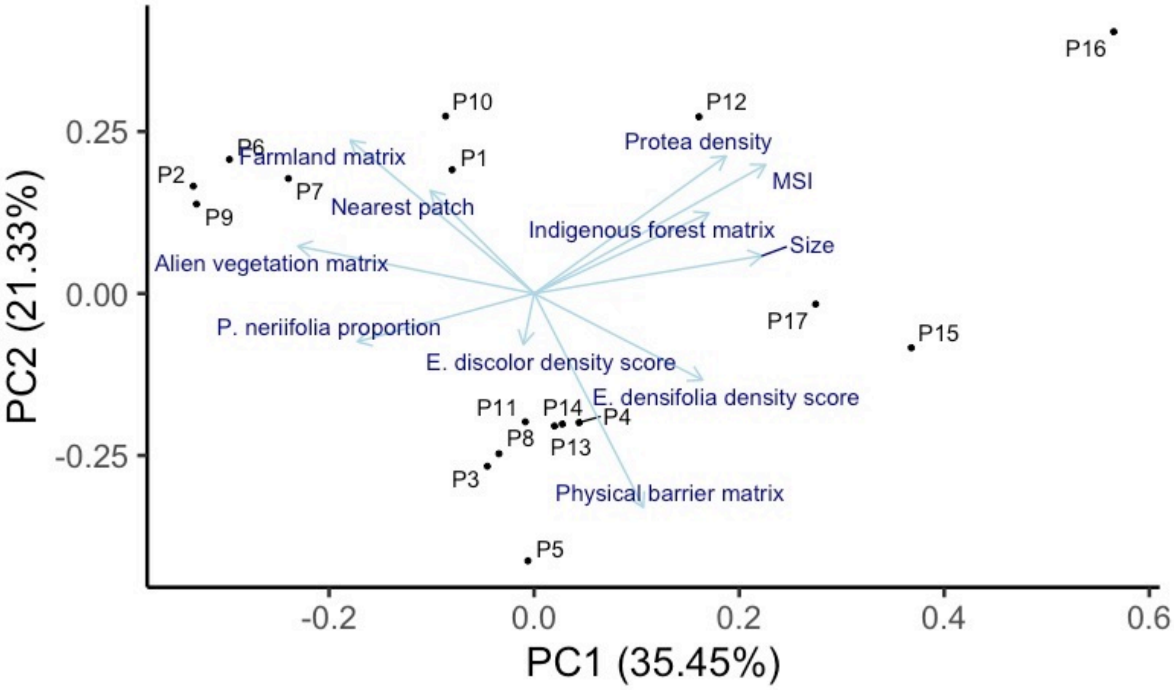


Figure 2.4: PCA biplot of the Tsitsikamma Plateau Fynbos study patches and loading vectors of the spatial and vegetation metric covariates.

For PC1, patch size, MSI, protea density and indigenous forest matrix had large positive loadings, whereas *P. neriifolia* proportion, alien vegetation matrix and farmland matrix had large negative loadings. *Protea neriifolia* proportion, as the inverse of *P. mundii* proportion, indicate that *P. mundii* would have had a high positive loading in PC1. Patches with positive PC1 were larger and more irregularly shaped, with high protea density, a higher *P. mundii* proportion and were surrounded by indigenous forest, whereas those with negative PC1 were smaller and rounder, with low protea density, a higher proportion of *P. neriifolia* and surrounded by alien vegetation and farmland (Figure 2.4). In PC2, physical barriers matrix had a large negative loading (also in relation to the magnitude of the positive loading PC2 covariates), and MSI, nearest patch, protea density, and farmland matrix had the largest positive loadings. Patches with negative PC2 had a high proportion of physical barriers matrix, were farther apart and had a rounder shape, and had lower protea density, whereas those patches with positive PC1 were closer to each other and had more irregular shapes, had a higher protea density and were surrounded by farmland (Figure 2.4). PC2 best described the proportion of the physical barriers' matrix surrounding patches in the study area, which was not correlated with size (unlike most PC1 covariates).

Discussion

To introduce the habitat fragmentation theme of the project, I did an exploratory PCA. In the PCA I analysed my 17 study patches in terms of their fragmentation metrics, surrounding matrix composition and attributes of focal protea and erica species (Table 2.4; Figure 2.4). The results show a clear distinction between the mostly larger, more intact fynbos patches with higher protea densities and a natural surrounding matrix, and smaller fragments of remaining habitat with lower protea densities and most with developed and disturbed surrounds. These patterns are expected of an anthropogenically fragmented landscape and can be explained by the 100+ years of development, habitat transformation, and other disturbances in the area (Kraaij et al. 2011, 2013a).

In a fragmented landscape, especially if it has been fragmented for a long time, you can expect that biodiversity and ecological systems, for example mutualistic relationships, may decline or break down (Hylander & Ehrlén 2013). This was shown, for example, when oil-secreting plants dependent on the oil-collecting bee *Rediviva peringueyi* for pollination failed to set seed in smaller habitat fragments in the western CFR once the bee was absent (Pauw 2007). By comparison, in the same smaller fragments, generalist plants with a suite of potential pollinators had high seed-set (Pauw 2007). Species movement and composition in especially smaller patches might be influenced and changed as a result of the surrounding disturbed and transformed habitat (Ewers et al. 2007; Betts et al. 2017). Tracking the movement of bird species in nine forest fragments in KwaZulu-Natal, South Africa, showed that dietary specialists rarely moved across the surrounding non-habitat matrix, whereas generalists and species that showed high movement ability were able to easily move between habitat patches (Neuschulz et al. 2013). However, researchers should be careful not to over-generalise the effects and influence of habitat fragmentation on a study system. Many factors can influence how a study system is affected, including the particular study species and habitat (Prugh et al. 2008; Betts et al. 2014). For example, as a highly mobile species that can easily travel over unsuitable habitat to reach woodland fragments, the Eastern Bettong (*Bettongia gaimardi*) in Tasmania, Australia, was not impacted by patch size and isolation, as long as their home range had enough suitable habitat patches (Gardiner et al. 2018).

In the rest of the study, I explored how the fragmentation patterns observed between my study patches influence the distribution and abundance of sunbirds and sugarbirds and the proteas and ericas they pollinate. However, it is important to understand the driving mechanisms responsible for any patterns found. This was shown in a study on the Eurasian Treecreeper (*Certhia familiaris*) in fragmented old forest habitat in central Finland. It was only after it was discovered that high nest predation rates associated with increased forest habitat, and not habitat fragmentation, was responsible for low fledging success that appropriate conservation action could be implemented (Le Tortorec et al. 2013). I thus aimed to understand and elucidate the driving mechanisms behind the patterns found in the study system so that the information gained can be applied towards targeted actions for conservation management.

Chapter 3: Patterns of avian species richness and abundance in a fragmented landscape: influence of patch and fragmentation variables

Abstract

Habitat fragmentation and other global change drivers brought about through human expansion and development are putting ecosystems and biodiversity at risk. The Cape Floristic Region (CFR) is restricted to the southern tip of southern tip of South Africa and is characterised by high species richness and endemicity. This lowland fynbos habitat has been highly fragmented through agriculture and other modified land uses. In this study in an area of fragmented fynbos habitat in the western Tsitsikamma in the eastern region of the Cape Floristic Region, I investigated the impact of habitat loss and fragmentation on bird species richness and nectar-feeding birds in fynbos habitat. I repeated 10-minute bird point-counts eight times over a year at 33 locations in 17 remnant fynbos habitat patches of differing sizes. Prior to each point-count I noted variables that could affect detection and noted vegetation variables in the immediate vicinity of the count location. For each patch I also determined erica and protea density and species proportions. I tested whether bird species richness and nectar-feeding bird abundance were influenced by fragmentation variables including patch size, isolation distance, surrounding non-habitat matrix, amount of fynbos habitat around a count location, the protea and erica patch variables, and the point-count detection and vegetation variables. Bird species richness was best explained by the influence of the surrounding matrix in combination with patch size. More species were recorded, and they accumulated at a faster rate, in small patches because of spill-over from adjacent habitats. General bird species richness was poorly explained by fragmentation, but fragmentation did explain nectarivore abundance between patches. Both fynbos endemic nectarivores, Cape Sugarbirds (*Promerops cafer*) and Orange-breasted Sunbirds (*Anthobaphes violacea*), were negatively affected by fragmentation, showing a lower probability of occurrence associated with a reduced amount of fynbos habitat surrounding a point-count location (the surrounding fynbos habitat increased with patch size). Malachite Sunbirds (*Nectarinia famosa*) were also less likely to be recorded as the extent of fynbos habitat surrounding a point-count location decreased. By comparison, the more habitat-generalist Amethyst (*Chalcomitra amethystina*), Greater Double-collared (*Cinnyris afer*), and Southern Double-collared Sunbirds (*Cinnyris chalybeus*) all increased in abundance as fynbos habitat decreased. I showed that habitat fragmentation has a negative effect on specialist fynbos bird species by reducing their habitat and by exposing them to pressures from the surrounding

matrix. Conservation and managing authorities should aim to conserve and expand on remaining fynbos habitat by clearing the surrounding non-habitat matrix of invasive alien vegetation and/or rehabilitation.

Introduction

Through their expansion and growth, humanity has brought about significant changes to the world's ecosystems and species, including through extensive habitat loss and fragmentation (McIntyre & Hobbs 1999; Hooke et al. 2012; Haddad et al. 2015; Maxwell et al. 2016). Researchers agree that habitat loss has a negative impact on biological systems and species, but more recently some researchers questioned the specific impact that the configuration of the remaining habitat has above the initial habitat loss (MacArthur & Wilson 1967; Fahrig 2003, 2013; Didham et al. 2012; Montero-Castaño & Vilà 2012). Overall though, in this well-studied field, the general long-term impact of habitat fragmentation is often negative for species richness, community composition and ecosystem functioning (Hadley & Betts 2012; Montero-Castaño & Vilà 2012; Haddad et al. 2015; Betts et al. 2017; Fardila et al. 2017; Aguilar et al. 2019; Horváth et al. 2019). Researchers though need to consider that many factors can affect the findings of a specific study (Ewers & Didham 2006; Pauw & Bond 2011; Driscoll et al. 2013).

In this chapter I investigate bird species richness and nectarivore abundance in and peripheral to the fragmented fynbos habitat patches of my study area in the eastern half of the species rich but highly fragmented Cape Floristic Region (CFR) (Rouget et al. 2003b; Mittermeier et al. 2011; Manning & Goldblatt 2012). Birds are popular for fragmentation research as shown by the extensive body of global research that use them as study subjects (Clark & May 2002; Fazey et al. 2005; Vargas et al. 2012; Fardila et al. 2017). Birds are not necessarily ideal study organisms for such studies, but they are easy to observe, cost effective to study and species have unique behaviour and characteristics that can be used to measure impact between different species (Fardila et al. 2017; Halstead et al. 2019). I focus on nectar-feeding bird species given their ecological importance as pollinators (Angoh et al. 2021). The study area contains two fynbos endemic nectarivores, Cape Sugarbirds (*Promerops cafer*) and Orange-breasted Sunbirds (*Anthobaphes violacea*), which play a vital role in pollinating a large proportion of CFR flowering species (Rebelo 1987; Brown 2005a, 2005b; Lee & Barnard 2016; Whitehead 2018), as well as a suite of habitat generalist species that are also associated with fynbos: Southern Double-collared (*Cinnyris chalybeus*), Malachite (*Nectarinia famosa*), Amethyst (*Chalcomitra amethystina*) and Greater Double-collared Sunbirds (*Cinnyris afer*) (Brown 2005c; Smith 2005; Smith & Tree 2005; Tree 2005; Whitehead 2018). The larger

Cape-Sugarbirds and Malachite Sunbirds exploit bird-pollinated proteas, of which *Protea neriifolia* and *Protea mundii* are the most abundant species in the study area (Brown 2005a, 2005c). The smaller species (primarily Orange-breasted and Southern Double-collared Sunbirds) feed extensively on erica nectar in fynbos, with *Erica discolor* and *Erica densifolia*, the two abundant bird-pollinated ericas in the study area (Brown 2005b; Smith 2005; Smith & Tree 2005; Tree 2005; Whitehead 2018).

I predict, according to Island Biogeography Theory, a marked reduction, or even disappearance, of some of the fynbos specialist nectarivore bird species in the smaller and/or more isolated patches where the absolute amount of habitat might be insufficient to support a species (Wilson et al. 2016). I aim to establish for species that are negatively affected by patch size and/or isolation, thresholds below which they are not able to persist. I further consider if the impact from fragmentation is better explained by the configuration of fragmented habitat patches or by the amount of remaining habitat as per the Habitat Amount Hypothesis (Fahrig 2003, 2013). I also predict that the overall bird species richness, as well as the presence and/or abundance of specific individual bird species reflects the influence of the surrounding matrix and the specific characteristics, behaviour, habitat use and preferences of a species i.e. habitat specialist or generalist (Wethered & Lawes 2005; Litteral & Wu 2012). I predict that this influence of the surrounding matrix is more pronounced in the smaller patches, as a larger proportion relative to size of the patch is exposed to the surrounding matrix (Ewers et al. 2007).

Methods

Study area, patch fragmentation metrics and protea/erica attributes

The study location is in a fragmented area of the southern Cape coast in the CFR. Chapter 2 describes the study area in the Tsitsikamma Plateau Fynbos, reports the methods used to choose and delineate the 17 study patches (Figures 2.2 and 3.1; Table 2.1) and describes the variables used in analyses. These variables record fragmentation metrics and focal protea and erica species attributes per patch. I also categorised the patches as small, medium or large and list the proportion of the different matrix habitats surrounding each patch (Table 2.1). In addition to the variables derived in Chapter 2, I created a binary variable based on patch size where the four patches > 150 ha were assigned to 'binary large patches' and the remaining 13 patches to 'binary small patches'. Using QGIS 3.1 (QGIS Development Team 2018) I also created buffer areas of radius 250 m, 500 m, 1000 m, 1500 m and 3000 m around the centroid of each patch. I did not use the latter three due to their strong correlation with the 500 m buffer area (based on calculated Pearson's product-moment correlation coefficients). For each radius distance I calculated the fynbos habitat amount (HA) surrounding a patch by clipping the patch's layer with the respective buffer areas. The HA for smaller patches included not only the fynbos habitat of the patch itself, but also habitat from surrounding patches (dependent on the buffer area used) that contributed to habitat potentially available for bird species.

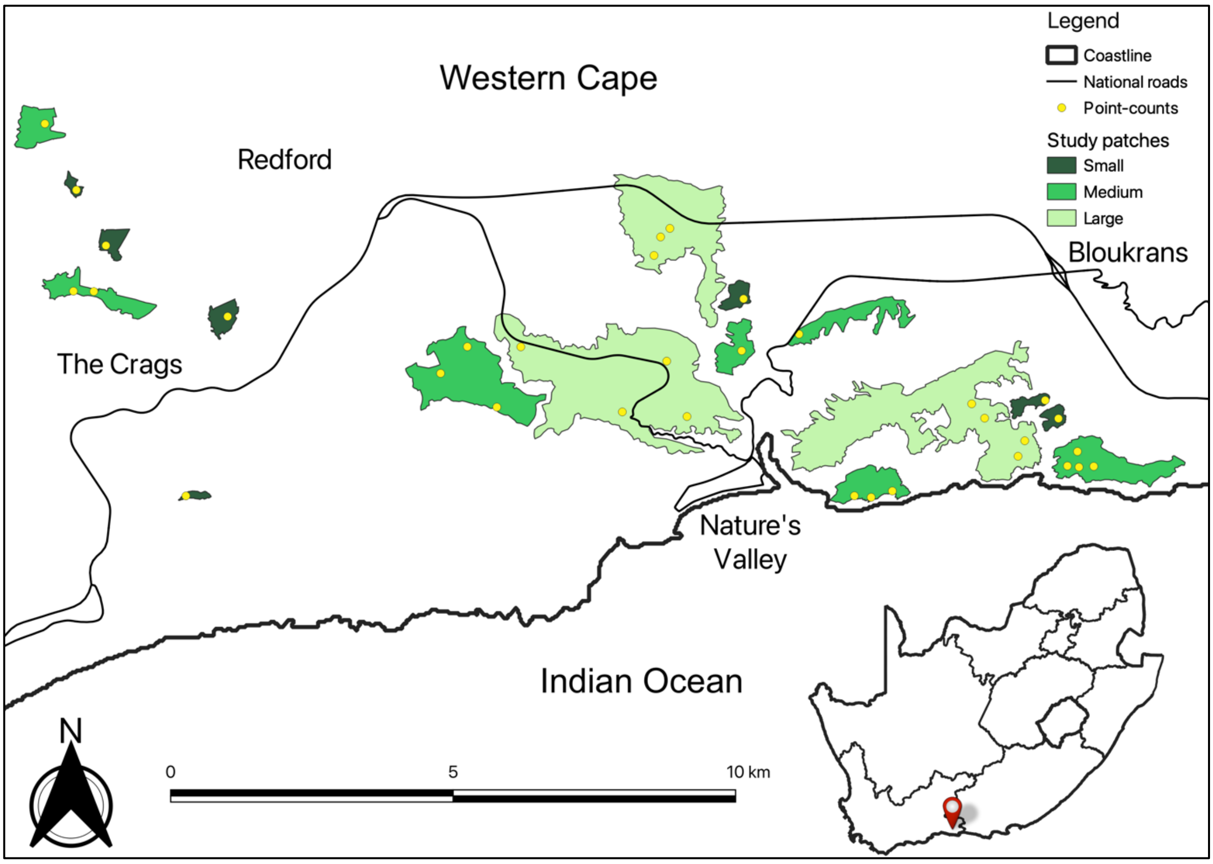


Figure 3.1: The 33 point-count locations in the 17 fynbos habitat patches in the southern Cape study area.

Fieldwork period and point-count surveys

I used a repeat-method point-count survey to sample the birds (Matsuoka et al. 2014; Miller et al. 2019). I adapted methods used by Lee et al. (2015) as I relied more on bird calls for identification because of the high and dense fynbos in the study area. I undertook several field trials to familiarise myself with all the bird species I was likely to encounter in my study area during sampling. To ensure that I could identify all the species by call, I studied the reference calls from Roberts VII multimedia birds of Southern Africa (Southern African Birding CC 2011) and Xeno-canto (Xeno-canto Foundation 2020). I undertook all point-counts myself to improve consistency and to minimise observer bias.

All point-counts were located away from roads to avoid features that could influence detection or a bird's calling, movements and behaviour (Geerts & Pauw 2011). I also positioned point-count locations at least 400 m apart to avoid the possibility of double-counting the same birds. Where present, I made use of existing animal and human tracks to move into accessible areas of a patch and between point-count locations. These choices and constraints resulted in only one point-count location for the smaller patches while for bigger patches I had up to four. That resulted in 33 point-count locations for the 17 patches (Figure 3.1). I recorded the coordinates of each point-count location using a Garmin eTrex 10 GPS to ensure that I conducted all repeats from the same locations.

My fieldwork period was 20 January 2016 to 8 February 2017. I surveyed each of the 33 point-count locations in eight repeat survey periods for a total of 264 point-counts (Table 3.1). It took approximately six weeks before I repeated a survey at a patch. I started all point-counts between 7h00 and 10h00 in summer, and 8h00 and 09h40 in winter. I only undertook point-counts on dry and wind-still (below a Beaufort wind scale of 3) days to minimise factors that could influence bird movement, calling and behaviour, and my ability to detect them.

Table 3.1: The start and finish dates for the eight survey periods where I repeated point-counts in each of the 17 study patches. SU – Summer, AU - Autumn, WI – Winter, SP - Spring

Survey period	**Date**	
	Start	**Finish**
1 - 1SU	20/01/2016	18/03/2016
2 – 2AU	07/04/2016	11/05/2016
3 – 3WI	02/06/2016	14/07/2016
4 – 4WI	18/07/2016	05/09/2016
5 – 5SP	07/09/2016	14/10/2016
6 – 6SP	27/10/2016	25/11/2016
7 – 7SU	05/12/2016	23/12/2016
8 – 8SU	18/01/2017	08/02/2017

Settling period and point-counts

During a five-minute settling period prior to each point-count I recorded site features for the immediate surroundings (15 m radius all-round). I recorded the height (0.25 m, 0.5 m, and in increments of 0.5 m thereafter) and proportion covered by each dominant vegetation species or functional category e.g. ericas (Siegfried & Crowe 1983). I ended with eight combined vegetation species/categories, that also include three low-count species/categories (less than 10 counts over 246 point-counts) that were incorporated into comparable species/categories. I calculated an overall vegetation height average (weighted by cover proportion and rounded to the closest 0.5 m), a biomass estimate for each vegetation species/category (height multiplied by cover proportion), and a total biomass estimate measure (sum of biomass for all species/vegetation categories). One category was pine (*Pinus* spp.) trees, and it is relevant to note that alien-vegetation eradication teams cleared many of the study patches of pines and other invasive plants shorty before my fieldwork period (M. Alant, SANParks pers. comm.). I also estimated and recorded environmental conditions and factors that could potentially influence bird movement, calling and behaviour and my ability to detect or identify them: noise levels (1 - neutral, 2 – persistent, 3 – loud, and 4 – very loud) and temperature [1 - cold (<9°C), 2 - mild (10 - 19°C), 3 – warm (20 - 29°C), 4 – hot (>30°C)].

During the 10-minute point-count, I recorded each individual or group (and the number of individuals) of all bird species that I saw or heard. I noted the time and estimated the distance from the point-count for each record. For birds seen I noted, where possible, the sex and age and if they were perched or flying. Outside of point-counts, I also noted additional incidental species observed while moving through the patches. I categorised each bird species according to foraging style, feeding guild, nectar usage and fynbos habitat use and preference, based on Hockey et al. (2005), Huntley & Barnard (2012), Lee & Barnard (2012) and Péron & Altwegg (2015).

Data analysis

I conducted analyses in R using the RStudio development framework and the "tidyverse" collection of packages for data science (Wickham et al. 2019; R Core Team 2020; RStudio Team 2022). I used the sf package to calculate the amount of fynbos habitat surrounding each point-count location (Pebesma 2018; R Core Team 2020). I first created 250 m and 500 m buffers around each point-count location and clipped these buffers to calculate the surrounding fynbos habitat amount. I used the vegan package function specaccum to estimate bird species accumulation curves from the point-count data (Oksanen et al. 2019). For the total bird species richness curve, I considered all species recorded and for the fynbos-typical species richness curve, only those species identified as such (Appendix 3.1). I also compared the species accumulation curves between three patch size categories (small, medium and large) by first including all the patches for each size category (seven patches each for small and medium, and three for large), and then with only three small and medium patches, selected at random, for a standardised comparison. I performed a cluster analysis using the R function hclust to visualise similarity of the 17 patches in terms of bird community composition. For the analysis I created a distance matrix of species and the number of times I observed each species across all point-counts for each patch. I explored similarity of patches in terms of bird species abundance using Principal Components Analysis (PCA) ordination for all birds recorded, fynbos-typical and nectarivore bird species abundance. I calculated bird species abundance from combined point-count data for each of the 17 study patches across the fieldwork year. I used the R function prcom to produce the PCAs, and the ggbiplot package to visualise them (Vu 2011).

I calculated correlations between the derived patch spatial and vegetation parameters using Pearson's product-moment correlation coefficients in the R function cor.test. Patch size was selected *a priori* as a variable of interest. I discarded perimeter, ED, HA 500, HA 1000 and HA 1500 because these parameters were all strongly correlated (all $p < 0.05$) with patch size. Proportions of *P. mundii* and *P. neriifolia* were strongly negatively correlated, so I considered only *P. neriifolia* for further analyses as it occurred at all patches. I created linear models to test the importance of the different patch, surrounding matrix and vegetation covariates on total, fynbos-typical and nectarivore only bird species richness as well as the presence of nectarivores endemic to (Cape Sugarbird, Orange-breasted Sunbird), or more strongly associated with, fynbos habitat (Malachite Sunbird and Southern Double-collared Sunbird). I used the Mantel test in the ade4 package to test (using 1000 Monte-Carlo permutations) for spatial autocorrelation in total, fynbos-typical and nectarivore bird species richness as recorded at all point-counts over the study period (Chessel et al. 2004; Dray & Dufour 2007; Dray et al. 2007; Bougeard & Dray 2018). One generated matrix for the Mantel test contained spatial distances and the other contained differences in species richness between the given points. Where I found spatial autocorrelation, I selected one point at random per patch for the models to account for it and to standardise effort. I applied an information theoretic approach to select the averaged model or best model by AICc from the set of candidate models using the dredge function from the MUMIn package (Anderson & Burnham 2002; Bartoń 2020). Summary tables report the top models within two AICc of the best-fit model and I illustrate the top candidate models within four AICc of the best model.

I fitted mixed-effects models to explore the contribution that variables that affect bird detection and that different patch, surrounding matrix and vegetation variables have on species richness and focal nectarivore species probability of occurrence between point-counts. I used the glmer function from the lme4 package with p values calculated using the lmerTest package (Bates et al. 2015), to fit models with a Poisson distribution for species richness and models with a binomial distribution for nectarivore species occurrence (Kuznetsova et al. 2017). I considered two highly correlated measures, groups of a species counted, and individuals detected during point-counts, as the response variable for nectarivore species occurrence. I used the former as it had the lowest variance of the two measures. Based on AIC, fitting models with a binomial distribution was best for nectarivore species probability of occurrence analyses. I created a binary measure for the analyses with 1 representing point-counts where I detected groups of a species and 0 where I did not. I used a model building philosophy based on information theory by adding variables piecewise and comparing AIC values between competing models. I selected the model with the lowest AIC value as the best-fitting model. In developing a model, I first tested if the detection variables should be included based on if they had a significant relationship with the response variable. I used the ncf package to test for spatial autocorrelation and if found added spatial coordinates as random effects to control for it (Bjornstad 2020). Next, to control for the variation of repeat counts at point-count locations over the fieldwork year I tested if I should include either survey period and/or point-count as random effects. This depended on if they had an influence on the response variable and then by which intercept only model performed best. From there I followed the forward selection philosophy starting with which habitat amount covariate performed best. I then tested the remaining explanatory variables starting *a priori* with the ones I considered most biologically relevant. Larger variables were centred and scaled before the models were run to improve fit. I also checked for collinearity using the cor.test function (Pearson's product-moment correlation) and removed any collinear variables from further models. I confirmed that the probability distribution used for each analyses was correct by examining the model residuals and Q-Q Plots of the "best" selected model using the qqpubr package (Kassambara 2020).

Following the snapshot paradigm of the distance sampling technique, I did not include birds flying through or flying in and perching during a point-count in the nectarivore distance analyses (Buckland et al. 2005). I pooled the eight point-counts conducted during the fieldwork year at each location and noted the visits as effort (following Buckland et al. 2008). I fitted detection models using the multi-covariate distance sampling engine in the Distance package (Buckland et al. 2005; Miller et al. 2019). The distance sampling engine selected the best model based on the lowest AIC value (Buckland et al. 2005). The models comprised combinations of key functions and adjustment terms (uniform with cosine or simple polynomial, half-normal with cosine or hermite polynomial, and hazard-rate with cosine or simple polynomial) (following Buckland et al. 2005). I stratified the results and present it by patch size category. I entered data as clusters for groups of birds (including groups of one). I used the distance sampling engine's size-bias regression procedure to correct for group size as a function of distance from the observer. I estimated the distance to each perched group to the nearest 10 m and truncated observations further than 100 m. I made use of the automated binning function of the distance sampling engine for distance intervals. I set CVMp > 0.2 for all species except for Southern Double-collared Sunbird where I had to set it to CVMp > 0.00001 for the models to run.

Results

Summary of bird records

I recorded 96 bird species during the 264 point-counts, with 2063 distinct species-records (first time recorded during a point-count). I recorded 4290 overall species records and 6889 birds if you include bird group numbers from records. Six of the species I could not positively identify, accounting for 36 distinct records (40 overall). Except for the species accumulation curves where I included all 96 bird species (see Species accumulation curves), I used the remaining 90 species (see Appendix 3.1), with 2027 distinct records and 4250 overall records, in further analyses. I recorded a further 31 species incidentally outside of point-counts while moving through the patches for an overall total of 121 identified species recorded during fieldwork (see Appendix 3.2). Just over a quarter of the species recorded during point-counts (24 of 90) are fynbos typical species, associated with fynbos habitat and a further 36 are known to use fynbos habitat to some extent (see Appendix 3.1). Eight of the species are specialist nectarivores, the pre-determined focal species for the study (see Appendix 3.1). I show the average distinct bird species records per patch/point-count during different time periods in Table 3.2. The species recorded and counted the most included mostly fynbos typical species e.g., Cape Sugarbird and Orange-breasted Sunbird, as expected from point-counts that were conducted in fynbos habitat (Table 3.3). Other non-fynbos typical species were loud and frequent calling species e.g., Southern Boubou (*Laniarius ferrugineus*) and Sombre Greenbul (*Andropadus importunus*), aerial specialist e.g., African Black Swift (*Apus barbatus*), or species just commuting over patches e.g., Black-headed Heron (*Ardea melanocephala*), not specifically associated with fynbos that are identified from the non-fynbos habitat surroundings and overhead (Table 3.3). Orange-breasted Sunbirds were completely absent from Patch 1, the smallest and most isolated of the 17 patches. Patches 2-4, the next three smallest patches, also had the next lowest counts for this species.

Table 3.2: Mean distinct bird species records during point-counts per patch/point-count and over different time periods.

Distinct species records $\bar{x}$ (SD)	Range	Patch/point-count	Period
11.1 (5)	4 – 25	point-count	patch visit
15.2 (5.3)	6 – 31	patch	
29.7 (7.1)	16 – 44	point-count	full fieldwork
38.5 (8)	23 – 55	patch	
52.9 (10.8)	37 - 66	patch	survey period

Table 3.3: The 10 species with the highest number of records (distinct detections) and with the most individuals recorded (including species group records). See Appendix 3.1 for the birds' scientific names.

Species	N records	Species	Total counted
Southern Double-collared Sunbird	478	Cape White-eye	1020
Cape Sugarbird	422	Cape Sugarbird	858
Orange-breasted Sunbird	403	Southern Double-collared Sunbird	558
Victorin's Warbler	337	Orange-breasted Sunbird	482
Karoo Prinia	283	Southern Boubou	392
Southern Boubou	254	Victorin's Warbler	353
Sombre Greenbul	176	Karoo Prinia	353
Cape White-eye	162	Sombre Greenbul	203
Cape Robin-chat	156	Amethyst Sunbird	173
Amethyst Sunbird	137	African Black Swift	166

Species accumulation curves

The species accumulation curves (SAC) based on all the point-count data included 96 bird species (Figure 3.2 A) and 24 fynbos typical species (Figure 3.2 B). The SAC for total bird species did not reach an asymptote after 264 point-counts (Figure 3.2 A), suggesting that additional species would have been recorded had fieldwork continued. For fynbos typical species the SAC flattened to a slope of 0.01 after 115 point-counts (Figure 3.2 B). The SACs show that I conducted enough point-counts to capture species richness patterns for fynbos typical but not for total bird species. I can explain the total bird species SAC not reaching an asymptote as it also includes many incidental non-fynbos habitat species from the diverse non-fynbos habitats surrounding the patches (Table 2.1; Appendix 3.1). For the SACs that grouped patches by size, when comparing the curves with all the patches in each size category (seven small and medium, and three large patches), the small patches accumulated species at the fastest rate, followed by medium and large patches (Figure 3.2 C). I found the same pattern when I compared the standardised groups but with negligible difference between large and medium patches (Figure 3.1 D). The faster accumulation rates for the small and medium patches reflect the contribution in species from the surrounding non-fynbos habitat matrix (Table 2.1; Appendix 3.1).

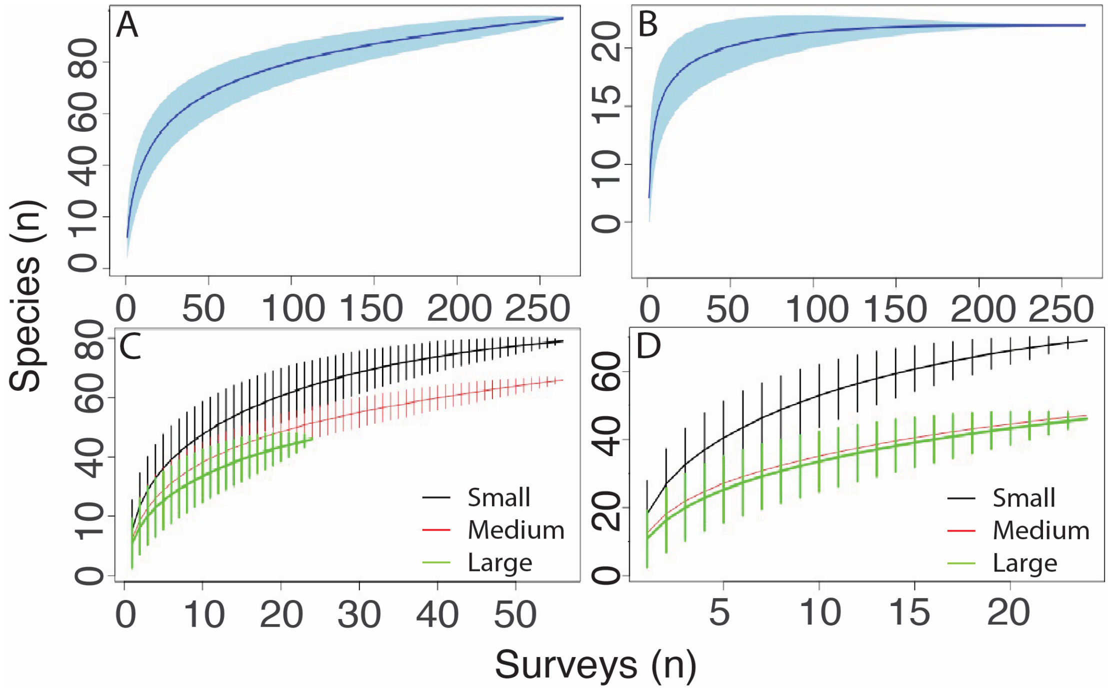


Figure 3.2: Species accumulation curves based on all the point-count data during the fieldwork period in the study area for all bird species (A) and for fynbos typical bird species (B). The further species accumulation curves compare between patch size categories for all the patches (C) and standardised on three patches per size category (D).

Patch similarity based on bird species composition

The cluster dendrogram indicated two distinct clusters of patches (Figure 3.3). A large-patch cluster that contains the three reference patches (Patches 15 - 17) and two of the larger medium-sized patches (Patches 11 and 13), which are all mostly surrounded by physical barriers and/or indigenous forest matrix (see Table 2.1). The two medium-sized patches and Patch 16 are the only patches that border on the coast (see Table 2.1). The smaller-patch cluster contains all other patches, which are all small or medium-sized, apart from Patches 12 and 14 that are two of the larger medium-sized patches (see Table 2.1). Most of smaller-patch cluster patches, in contrast to the large-patch cluster, are surrounded by a modified matrix of farmland and/or alien vegetation (apart from Patch 1 that is surrounded by indigenous forest) with a different cohort of bird species (see Table 2.1).

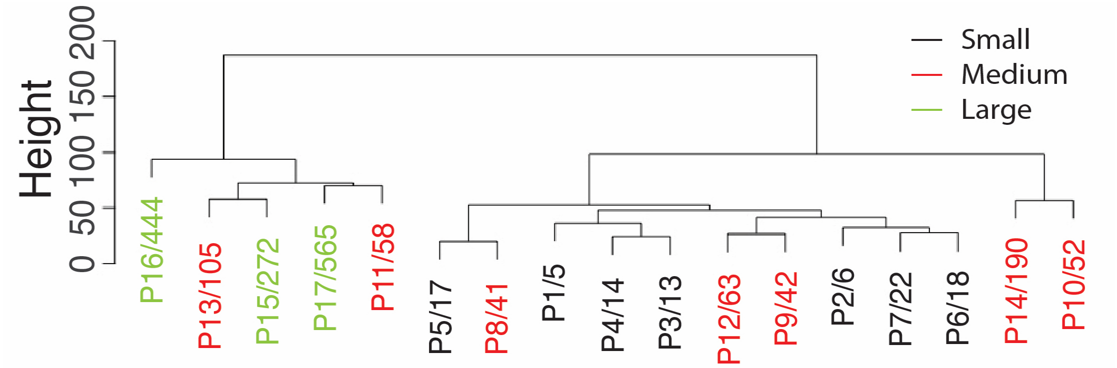


Figure 3.3: A cluster dendrogram that illustrates the similarity of patches based on bird species composition. Patches are numbered by size (S1 smallest to S17 largest) and size (ha).

In all three PCAs relating patch similarity to bird abundance, PC1 explained over 75% of the total variance. I focussed only on PC1 to describe similarity patterns among patches. In all three PCAs the birds with the highest loadings (all positive) were mostly fynbos-typical species (Table 3.4). The exception was the Southern Boubou, an abundant thicket species (Merkle 2010). I likely picked the species up because of its loud and conspicuous call, audible from surrounding habitats, and/or because the mature fynbos is becoming more suitable as habitat (Merkle 2010). The two fynbos endemic nectarivores, Cape Sugarbird and Orange-breasted Sunbird, had the highest loadings (Table 3.4; Figure 3.4). Patches on the positive PC1 loading side for all three PCAs were larger-sized patches surrounded by indigenous forest matrix and with little alien vegetation and farmland matrix around them (Figure 3.4; Table 2.1). Patches on the negative PC1 loading side were mostly smaller-sized with a mix of surroundings of which there are higher proportions of alien vegetation and farmland matrix (Figure 3.4; Table 2.1). The medium and large patches on the positive loading side of the PCAs (patches 11, 13, 15-17; Figure 3.4) were all located in the large-patch clusters of the cluster diagram (Figure 3.3). I could not discern a clear relationship with patch size for fynbos non-typical species

(Appendix 3.1; Table 3.4) likely because the large patches have more fynbos habitat around the points-counts and the small and medium patches are surrounded by a diversity of matrices that are each associated with different bird species (Kennedy et al. 2010; Öckinger et al. 2012a, 2012b).

Table 3.4: The loadings for the two component axes extracted from each of the three bird-species related PCA analyses; nectarivore, fynbos typical and all species, and the percentage of variation explained by each component. * - only species with a loading from ± 0.01 on PCA 1 or ± 0.03 on PCA 2 except for species that are also fynbos typical or nectarivore. The list is sorted by PC1 loadings. See Appendix 3.1 for the birds' scientific names.

Species	**Nectarivore**		**Fynbos Typical**		**All species***	
	PC1	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
	(82.4%)	**(8.0%)**	**(81.8%)**	**(6.1%)**	**(75.4%)**	**(7.5%)**
Cape Sugarbird	0.67	-0.55	0.53	-0.72	0.51	0.22
Orange-breasted Sunbird	0.63	0.71	0.51	0.4	0.49	0.31
Southern Double-collared sunbird	0.3	-0.15	0.25	0.21	0.25	-0.55
Malachite Sunbird	0.23	-0.14	0.19	-0.18	0.18	0.07
Amethyst Sunbird	0.02	-0.3			0.01	-0.14
Greater Double-collared Sunbird	-0.008	-0.29	-0.008	-0.17	-0.006	-0.16
Collared Sunbird	-0.005	-0.007			-0.004	-0.003
Grey Sunbird	-0.005	-0.01			-0.004	-0.01
Victorin's Warbler			0.42	0.05	0.41	-0.08
Karoo Prinia			0.39	0.37	0.38	0.03
Cape Grassbird			0.15	-0.12	0.14	0.12
Cape Robin-chat			0.08	0.03	0.08	-0.22
Bar-throated Apalis			0.07	0.14	0.07	-0.13
Cape Siskin			0.03	0.05	0.03	-0.003
Yellow Bishop			0.03	-0.04	0.03	0.05
Cape White-eye			0.02	-0.16	0.02	-0.13
Red-necked Spurfowl			0.02	-0.03	0.02	0.03
Brimstone Canary			0.01	-0.04	0.01	-0.02
Grey-backed Cisticola			0.01	-0.04	0.01	0.02
Common Waxbill			0.0005	-0.008	0.0006	-0.009
Cape Weaver			-0.006	-0.02	-0.006	-0.007
Cape Bulbul			-0.003	-0.03	-0.003	-0.05
Cape Canary			-0.003	0.005	-0.003	0.002
Streaky-headed Seedeater			-0.003	0.21	-0.003	0.01
Neddicky			-0.00005	-0.009	0.001	-0.09
Lazy Cisticola					0.05	0.04
African Black Swift					0.02	-0.02
Barn Swallow					0.02	-0.07
Black Saw-wing					0.02	-0.05
Greater Striped Swallow					0.02	-0.04
Cape Batis					0.01	0.003
Hadada Ibis					0.007	-0.04
Black-headed Oriole					0.004	-0.05
Knysna Turaco					0.003	-0.1
Cape Turtle Dove					0.0004	-0.09
Egyptian Goose					-0.01	-0.06
Fork-tailed Drongo					-0.01	-0.12
Red-eyed Dove					-0.008	-0.07
Forest Canary					-0.006	-0.03
Olive Bushshrike					-0.005	-0.04
Red-chested Cuckoo					-0.004	-0.03
Helmeted Guineafowl					-0.002	-0.04

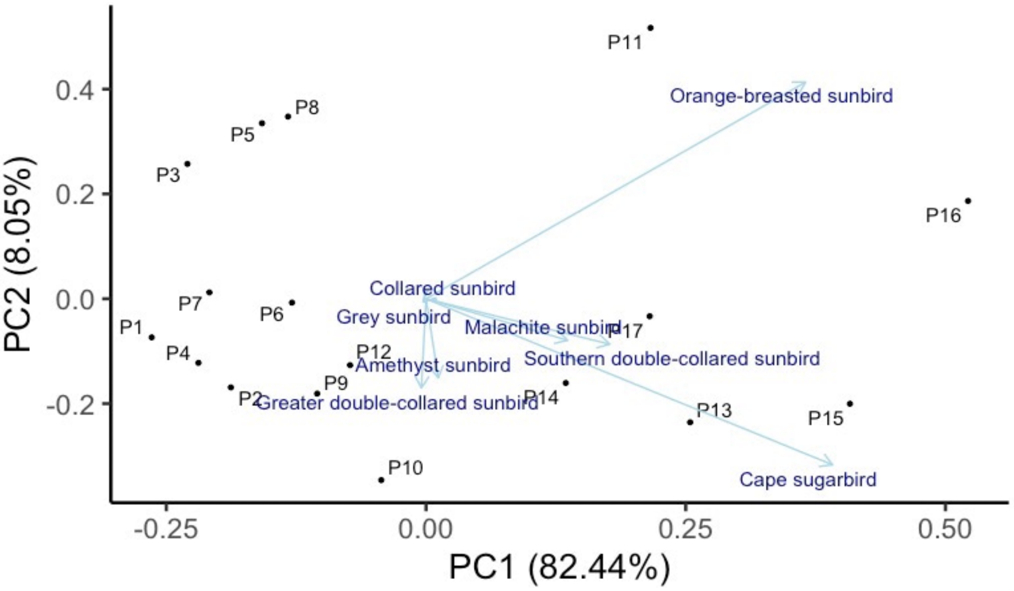


Figure 3.4: A biplot of the study patch scores for the 17 patches and nectarivore birds loading vectors for PCs 1 and 2.

Bird species richness and nectarivore presence

I controlled for spatial autocorrelation between point-counts for total bird species richness in the model (r = 0.37, p = 0.0002; Appendix 3.3 A). Neither fynbos-typical (r = 0.078, p = 0.15) nor nectarivore (r = -0.017, p = 0.56) species richness showed spatial autocorrelation, with some exception in the southeast quadrant for nectarivore species richness (Appendix 3.3 B). The proportion of patch perimeter with physical barriers was a significant negative predictor in the model explaining total bird species richness among patches (Figures 3.5 A; Table 3.5 and Appendix 3.4). This is because the physical barrier matrix has less potential to contribute species than other matrix types while the three other matrix categories all contribute meaningfully to patch species richness with, for example, Knysna Turaco and Green-backed Camaroptera associated with indigenous forest matrix (see Table 2.1; Hockey et al. 2005; SANParks 2017). None of the patch descriptive variables in the averaged models explained fynbos-typical species richness or nectarivore species richness among patches. The lack of explanatory power of the attributes used in the species richness models is probably because of the small sample size (only 17 of the 33 point-count points were used). I also suggest that the influence of the surrounding matrix can explain why no explanatory variables explain fynbos-typical or nectarivore bird species richness among patches. Many of the fynbos-typical bird species not only associate with fynbos, but also with surrounding matrix habitats. For example, Cape White-eyes and Cape Weavers are also associated with the farmland matrix (Mangnall & Crowe 2003; Hockey et al. 2005). Among the specialist nectarivores, only Orange-breasted Sunbirds and Cape Sugarbirds are associated predominantly with fynbos, whereas others such as the Greater and Southern Double-collared Sunbirds are habitat generalists that visit fynbos in search of suitable food sources (Brown 2005a, 2005b; Smith 2005; Smith & Tree 2005). Considering the four nectarivore bird species strongly associated with fynbos habitat, the presence of Malachite Sunbirds was best explained by patch size (binary variable; Figure 3.5 B; Table 3.5). They are more likely to be found in large patches that have a high proportion of fynbos habitat surrounding the point-count location. For Cape Sugarbirds, nearest patch and *P. neriifolia* proportion were the most significant and biologically relevant predictors in the averaged model (Figure 3.5 C; Table 3.5). I inferred from this that the presence of *P. mundii* (the protea that occurs in inverse abundance to *P. neriifolia*) is a strong predictor of Cape Sugarbird presence in a patch over the fieldwork year. I found *P. mundii* in only six of the 17 patches, but on some of the larger patches (e.g., Patches 12, 15 and 16) they grow densely and produce large numbers of flowers. The abundant *P. mundii* on these patches seemingly had a disproportionate effect on the association found in the analysis. Several covariates were significant in the single best model for Orange-breasted Sunbirds (Figure 3.5 D; Table 3.5), but after plotting the relationships, none had meaningful interpretation. None of the patch descriptive variables in the averaged model explained Southern Double-collared Sunbird presence across the patches.

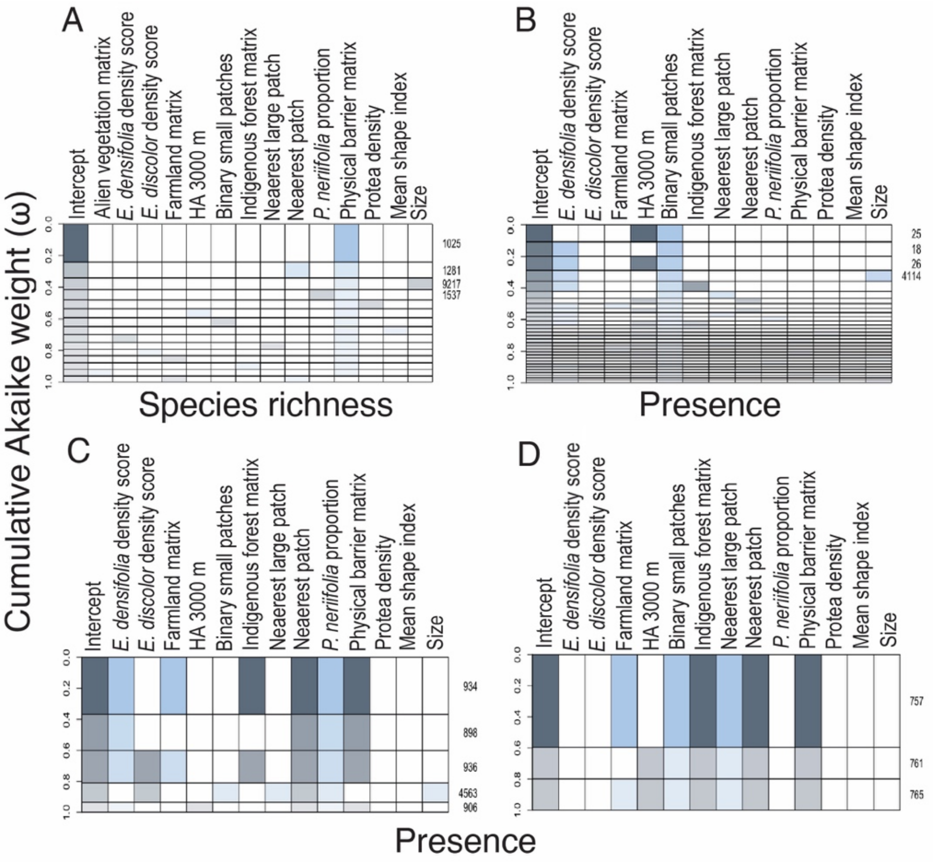


Figure 3.5: Model selection tables that show the number of models that each covariate is included in and its value, based on shading density, as an explanatory variable for species richness (A) and Malachite Sunbird (B), Cape Sugarbird (C) and Orange-breasted Sunbird (D) presence between the 17 study patches.

Table 3.5: Summary table of model coefficients for models explaining species richness or presence of individual species across the 17 study patches. The test statistic for averaged model is a z-score and for the single model it is a t-value. P-values lower than 0.05 are highlighted in bold. The number in brackets for the averaged models, is the number of models within two AICc points of the top-performing model.

Metric	Model	Coefficients	Estimates	SE	t/z value	Pr(>|t/z|)
Species richness	average (two)	intercept	39.55	2.52	15.68	**<0.001**
		physical barrier matrix	-18.53	4.98	3.72	**<0.001**
		nearest patch	0.82	1.91	0.43	0.68
Malachite Sunbird	average (six)	intercept	2.88	0.7	3.96	**<0.001**
		HA 3000 m	-0.15	0.21	0.69	0.49
		binary small patches	-1.44	0.54	2.51	**0.012**
		E. densifolia density	-0.31	0.28	1.06	0.27
		patch size	-0.00032	0.0009	0.35	0.73
		indigenous forest matrix	-0.094	0.29	0.32	0.75
		nearest large patch	0.0083	0.029	0.28	0.78
Cape Sugarbird	average (three)	intercept	7.8	1.67	4.54	**<0.001**
		nearest patch	-1.19	0.29	3.64	**<0.001**
		E. densifolia density	-0.44	0.13	3.23	**0.001**
		farmland matrix	-3.52	2.53	1.35	0.18
		indigenous forest matrix	-1.48	1.07	1.35	0.18
		physical barrier matrix	-3.32	1.58	2.05	**0.04**
		P. neriifolia proportion	-2.73	0.6	4.35	**<0.001**
		E. discolor density	0.08	0.14	0.53	0.6
Orange-breasted Sunbird	single	intercept	7.35	0.92	8.0	**<0.001**
		nearest large patch	-0.36	0.071	-5.04	**<0.001**
		nearest patch	-1.53	0.57	-2.67	**0.008**
		farmland matrix	-5.51	1.64	-3.36	**<0.001**
		binary small patches	0.91	0.24	3.78	**<0.001**
		indigenous forest matrix	-3.78	0.77	-4.95	**<0.001**
		physical barrier matrix	-6.59	1.31	-5.03	**<0.001**

Species richness patterns and nectarivore probability of occurrence

In the mixed-effect model that relates species richness to patch, surrounding matrix and vegetation covariates, I controlled for spatial autocorrelation found in species richness across the point-counts (Appendix 3.5). Point-count ($\chi^2 = 193.7$, $p < 0.001$; Appendix 3.6) and survey period ($\chi^2 = 52.9$, $p < 0.001$; Appendix 3.7), but not their interaction ($\chi^2 = 129.3$, $p = 1$), had a significant effect on bird species richness. As the intercept-only model performed best with point-count and survey period, I included both as random effects in further models. I did not include detection variables in further models as none I tested had a significant relationship with species richness (noise level: z-value = -1.098, p = 0.272; temperature: z-value = 0.702, p = 0.483; weighted vegetation height: z-value = 0.299, p = 0.765). In the "best" model, fynbos habitat within 500 m was a significant negative predictor and pine trees a significant positive predictor of species richness between the point-counts (Table 3.6; Figure 3.6). Patch size was correlated with fynbos habitat amount within 500 m (R = 0.77, t = 4.66, p-value = 0.0003), which indicated that the point-counts with the higher proportion of fynbos habitat around them are the large and medium patches. The high correlation was more a reflection of the smaller spatial scale of the study than that habitat amount was more applicable for analysis (Bueno &

Peres 2019). The negative relationship of species richness with fynbos habitat within 500 m also illustrated the influence of the surrounding non-fynbos habitat matrix on species richness. The positive relationship of species richness with pine trees was also indicative of the influence of the surrounding matrix and possibly also because of the added habitat complexity added by the trees (Table 3.6; Figure 3.6). A range of non-fynbos bird species are associated and benefit from pine and other tall, woody invasive alien vegetation (Allan et al. 1997; Wethered & Lawes 2003, 2005). Ten of the 17 patches had some alien vegetation matrix (including pine plantations) on their peripheries, a source of pine and other alien invasive trees to the fynbos habitat (Table 2.1). As alien invasive trees were removed from most patches prior to the study, the positive relationship of species richness with pine trees was more a reflection of the impact of the surrounding alien matrix on bird species richness than that the patches were invaded by alien vegetation.

Table 3.6: Model coefficients summary table for models explaining species richness and probability of occurrence of individual species across the point-counts as a function of detection covariates. P-values < 0.05 are highlighted in bold.

Model	**Spatial autocorrelation correction**	**Coefficients**	**Estimate**	**Standard error**	**z-value**	**Probability (>|z|)**
Species richness	X-coordinate	intercept	2.45	0.054	45.61	**<0.001**
		HA 500 m	-0.13	0.033	-3.85	**<0.001**
		pine trees	0.21	0.078	2.68	**0.007**
Cape Sugarbird	N/A	intercept	0.5	0.35	1.42	0.15
		HA 500 m	0.57	0.18	3.27	**0.001**
		P. neriifolia biomass	0.95	0.19	4.86	**<0.001**
Orange-breasted Sunbird	N/A	intercept	1.42	0.51	2.81	**0.005**
		HA 250 m	1.35	0.37	3.61	**<0.001**
		erica biomass	0.88	0.31	2.88	**0.004**
Southern Double-collared Sunbird	N/A	Intercept	2.27	0.39	5.78	**<0.001**
		HA 250 m	-0.45	0.29	-1.52	0.13
		erica biomass	0.22	0.25	0.85	0.39
Malachite Sunbird	N/A	intercept	-.1.15	0.53	-2.15	**0.032**
		HA 500 m	0.6	0.19	3.2	**0.0014**
		P. neriifolia biomass	0.006	0.0043	1.4	0.16
		M. muricata biomass	-0.01	0.005	-2.022	**0.043**
Amethyst Sunbird	X-coordinate	intercept	0.59	0.6	0.98	0.33
		temperature	-0.64	0.2	-3.21	**0.001**
		noise level	-0.68	0.24	-2.88	**0.004**
		hour	-0.77	0.21	-3.71	**<0.001**
		HA 500 m	-0.28	0.2	-1.45	0.15
		P. neriifolia biomass	0.59	0.19	3.11	**0.002**
		pine trees	1.59	0.56	2.83	**0.005**
Greater Double-collared Sunbird	N/A	intercept	-1.09	0.36	-2.99	**0.003**
		HA 500 m	-0.66	0.25	-2.61	**0.009**
		erica biomass	0.21	0.21	0.99	0.32

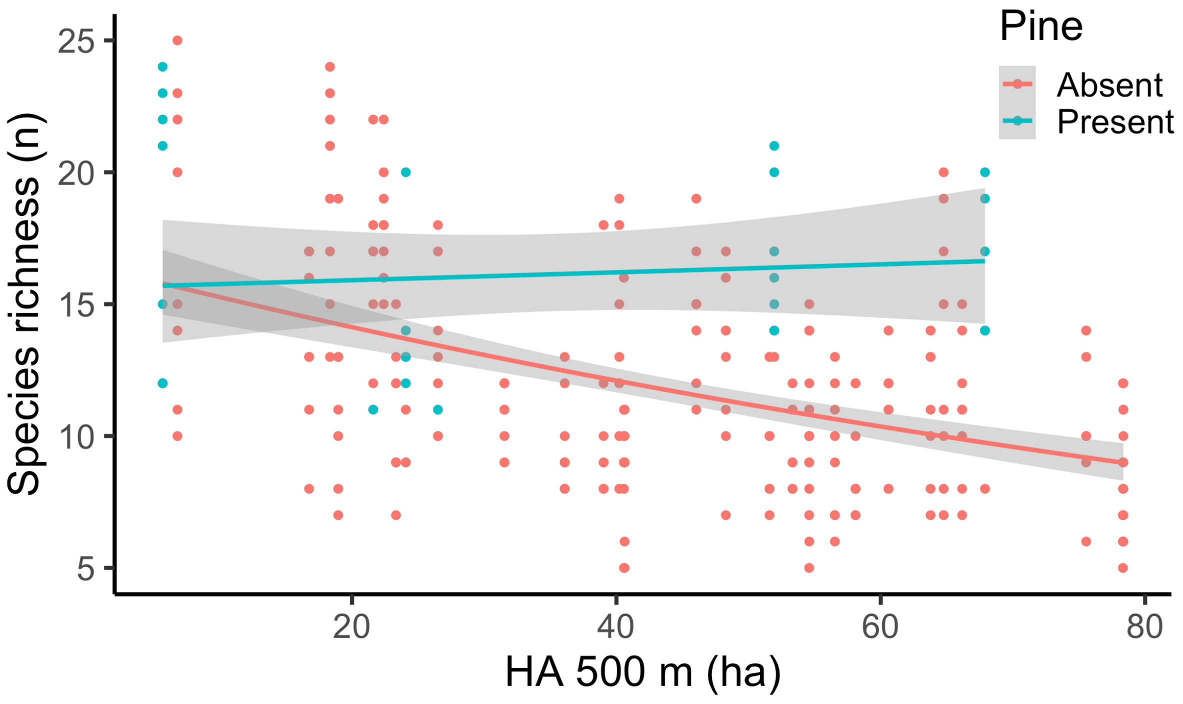


Figure 3.6: The relationship of species richness with fynbos habitat within 500 m of a point-count, with or without pine trees present. I display best-fit lines and standard error bands.

Only six of the eight nectarivore species detected in point-counts during the fieldwork year had sufficient records for analyses (Southern Double-collared Sunbird - 642, Orange-breasted Sunbird - 540, Cape Sugarbird - 533, Amethyst Sunbird - 188, Malachite Sunbird - 177, and Greater Double-collared Sunbird - 154); only four Grey Sunbirds and three Collared Sunbirds were counted. For each of the species analysed, point-count and survey period, but not their interaction, had a significant effect on probability of occurrence. I included both as random effects in further models. The probability of occurrence for Cape Sugarbird around a point-count was positively influenced by fynbos habitat within 500 m (HA 500 m Figure 3.7 A.1) as well as *P. neriifolia* biomass (Figure 3.7 A.2; Table 3.6). Malachite Sunbird showed a similar pattern to Cape Sugarbird in that its probability of occurrence increased with fynbos habitat within 500 m around a point-count (Figure 3.7 B.1; Table 3.6), and there was a non-significant tendency to increase with *P. neriifolia* biomass (Figure 3.7 B.2; Table 3.6). A high biomass of *Metalasia muricata* (a non-bird pollinated member of the Asteraceae family and one of the vegetation species counted around point-counts) tended to decrease Malachite Sunbird probability of occurrence, presumably because they prefer more open vegetation (*M. muricata* can grow densely) and/or higher biomass *M. muricata* results in less protea and erica availability (Figure 3.7 B.3; Table 3.6).

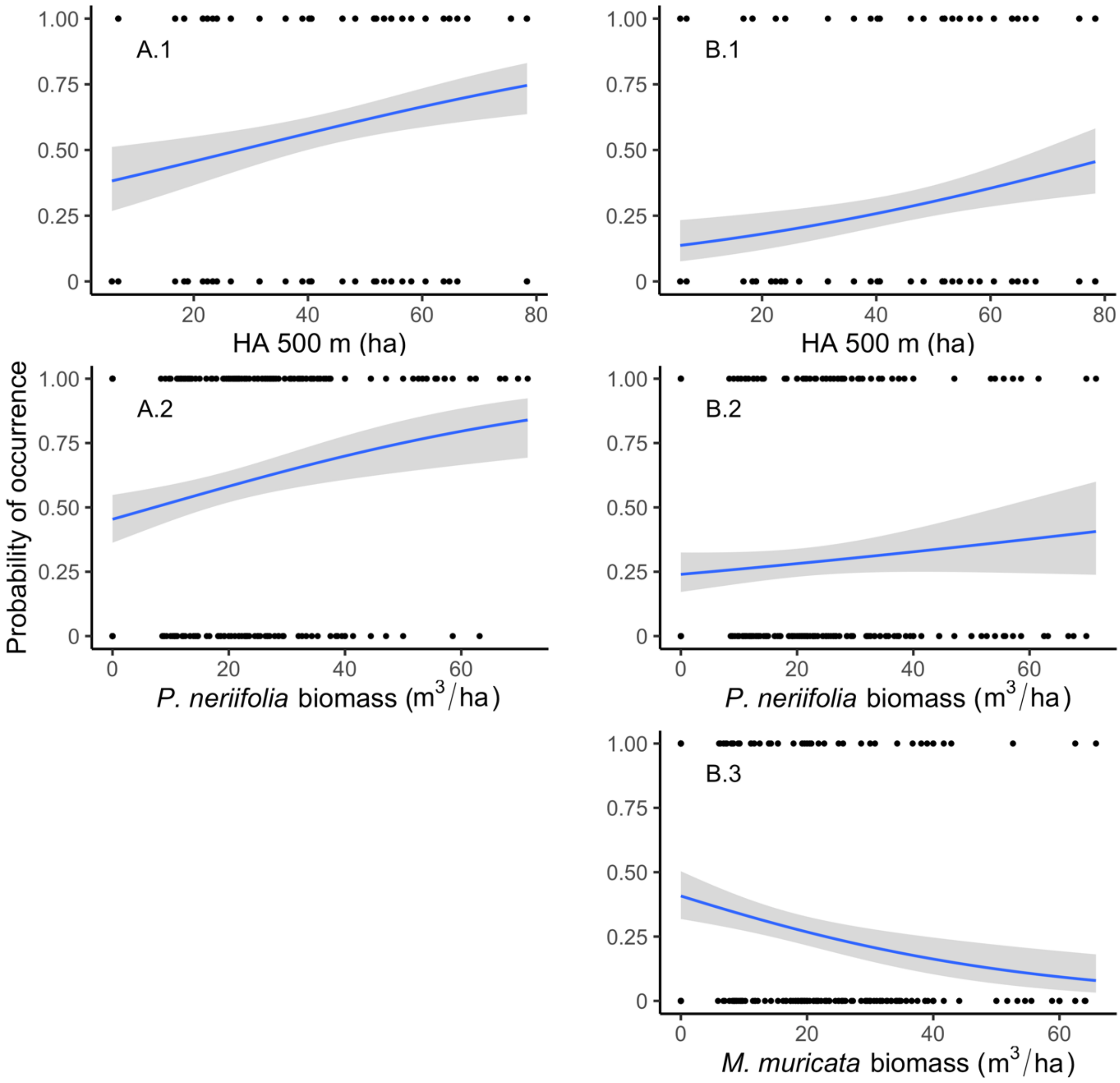


Figure 3.7: Cape Sugarbird (A) and Malachite Sunbird (B) probability of occurrence around a point-count as related to fynbos habitat within 500 m (A.1) and *P. neriifolia* biomass (A.2) for the former and habitat within 500 m (B.1), *P. neriifolia* biomass (B.2), and *M. muricata* biomass (B.3) for the latter. The *P. neriifolia* biomass relationship with Malachite Sunbird is non-significant. I display best-fit lines and standard error bands for each relationship.

Orange-breasted Sunbird probability of occurrence increased with an increase in fynbos habitat within 250 m (Figure 3.8 A.1) and erica biomass surrounding a point-count (Figure 3.8 A.2; Table 3.6). The probability of occurrence of Southern Double-collared Sunbirds on the other hand, non-significantly decreased with fynbos habitat within 250 m (Figure 3.8 B.1) and non-significantly increased with erica biomass around a point-count (Figure 3.8 B.2; Table 3.6).

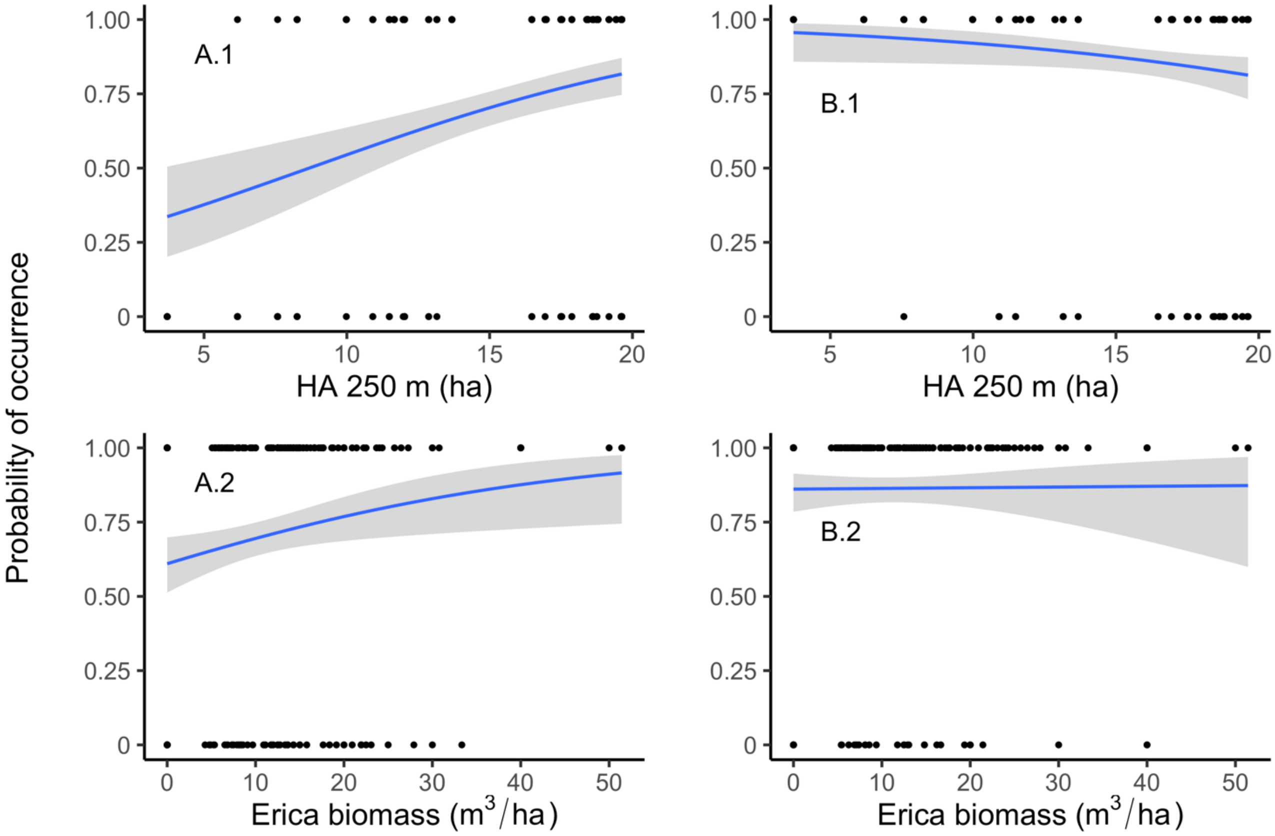


Figure 3.8: Orange-breasted (A) and Southern Double-collared Sunbird (B) probability of occurrence around a point-count as related to fynbos habitat within 250 m (A.1) and erica biomass (A.2) for the former and fynbos habitat within 250 m (B.1) and erica biomass (B.2) for the latter. Both Southern Double-collared Sunbird relationships are non-significant. I display best-fit lines and standard error bands for each relationship.

Only the Amethyst Sunbird of the species analysed had spatial autocorrelation between the point-counts and that the detection variables tested had a significant relationship with its probability of occurrence (Appendix 3.8; Table 3.6). I accounted for both aspects in the Amethyst Sunbird's models (Table 3.6). The probability of occurrence for Amethyst Sunbird was non-significantly negative with fynbos habitat within 500 m (Figure 3.9 A.1), and significantly positively related to *P. neriifolia* biomass (Figure 3.9 A.2) and pine trees (Figure 3.9 A.3) around a point-count (Table 3.6). Greater Double-collared Sunbird probability of occurrence was negatively related to an increase in fynbos habitat within 500 m of a point-count (Figure 3.9 B.1; Table 3.6). A non-significant relationship suggested that it was positively related to erica biomass (Figure 3.9 B.2; Table 3.6).

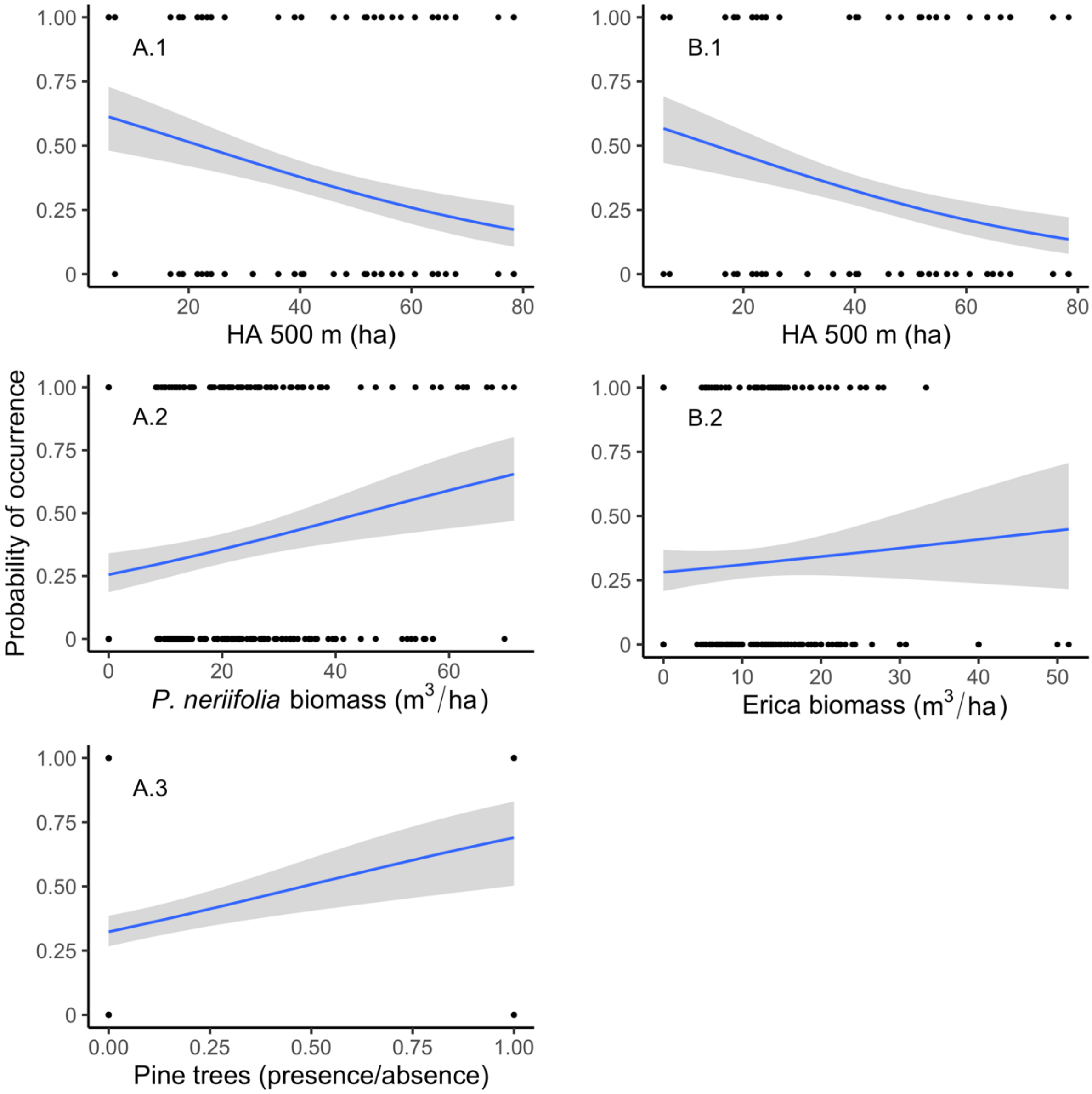


Figure 3.9: Amethyst (A) and Greater Double-collared Sunbird (B) probability of occurrence around a point-count as related to fynbos habitat within 500 m (A.1), *P. neriifolia* biomass (A.2) and pine trees (A.3) for the former and fynbos habitat within 500 m (B.1) and erica biomass (B.2) for the latter. The relationships of fynbos habitat within 500 m with Amethyst Sunbird and erica biomass with Greater Double-collared Sunbird are non-significant. I display best-fit lines and standard error bands for each relationship.

Nectarivore density differences between patch size categories

The results of the density estimates are not that conclusive as there was not a lot of data that was suitable for the analyses. In the analyses only Amethyst Sunbird had an average covariation range under the threshold of 0.2 that suggests a reasonable result (Table 3.7) (Marsden 1999). Southern Double-collared and Orange-breasted Sunbirds also came close to this threshold (Table 3.7). Of the six specialist nectarivores, Southern Double-collared Sunbird (209.1 individuals·km^{-2}), Cape Sugarbird (112.8 km^{-2}) and Orange-breasted Sunbird (86.3 km^{-2}) had the highest average densities, while Amethyst Sunbird (59.2 km^{-2}), Malachite Sunbird

(22.3 km^{-2}) and Greater Double-collared Sunbird (17.1 km^{-2}) were less abundant (Table 3.7). Southern Double-collared Sunbird and Amethyst Sunbird had lower densities as the patch size category increased (Table 3.7). Cape Sugarbird density tended to be lower in larger patches (Table 3.7). I can possibly explain Cape Sugarbirds lower density in the larger patches by considering that their territorial behaviour potentially prevents them from reaching their potential maximum densities in the large patches with high density of proteas (Calf et al. 2003a). Orange-breasted (Appendix 3.9) and Greater Double-collared Sunbird densities increased with patch size (Table 3.7). Malachite Sunbird densities did not show a clear pattern with patch size (Table 3.7).

Table 3.7: Local density estimates (individuals·km^{-2}) for six nectarivores. SE = Standard error; LCL and UCL = lower and upper 95% confidence intervals of density estimates; CV = coefficient of variation of model fit; n = number of detections; Average probability = probability of detection.

Species	**Size categories**	**Density**	**SE**	**LCL**	**UCL**	**CV**	**Degrees of freedom**	**Average density**	**n**	**Average probability**	**SE**	**CV**
Cape Sugarbird	S	127.1	93.9	30.8	525.1	0.7	13.7	112.8	43	0.1	0.03	0.4
	M	125.6	73.1	42.4	372.2	0.6	47.1					
	L	85.6	50.2	28.5	257.4	0.7	37					
Orange-breasted Sunbird	S	35.7	24.3	8.4	151.1	0.7	7.4	86.3	48	0.2	0.03	0.2
	M	86.1	31.4	41.8	177.3	0.4	29.8					
	L	140.1	67.8	52.8	371.7	0.5	15.2					
Southern Double-collared Sunbird	S	333.1	186.7	100.5	1104.2	0.6	8.3	209.1	46	0.04	0.01	0.2
	M	184.2	70.2	86.7	391.4	0.4	28.6					
	L	109.9	73	29.6	407.8	0.7	12.5					
Malachite Sunbird	S	27.6	21.8	5.6	135.5	0.8	8.4	22.3	19	0.1	0.05	0.3
	M	9.2	5.3	3.1	27.5	0.6	24.7					
	L	30.1	17	10	90.7	0.6	18.7					
Amethyst Sunbird	S	126.7	59.8	44	365.2	0.5	7.1	53	18	0.3	0.05	0.1
	M	28	14	10.3	76.3	0.5	16.1					
	L	4.2	4.3	0.7	27.2	1	10.4					
Greater Double-collared Sunbird	S	8.1	15.3	0.5	134	1.7	8.6	17.1	7	0.1	0.1	1.6
	M	22.7	39.4	1.4	372	1.7	6.9					
	L	20.6	35.7	1.3	339.3	1.7	6.8					

Discussion

Patch size, as predicted, affected fynbos bird nectarivore occurrence, with the two fynbos endemic nectarivores negatively affected. Species richness, also as predicted, strongly reflected the influence of the surrounding matrix, especially in the smaller patches. However, contrary to expectations, the distance between patches had little explanatory power, presumably because the distances between patches are too small and/or the matrix is not enough of a deterrent to prevent birds from moving among patches (Bélisle & St. Clair 2002). The influences of patch size and distance between patches are thus confounded. The absence of Orange-breasted Sunbirds from the smallest and most isolated patch, suggests that distance between patches might have been a factor. My study patch configuration did not lend itself to explore this further. I also wanted to determine if the amount of habitat around a point-count or the configuration of patches had the most explanatory power. I found though in the study that they were correlated and could thus not further differentiate their explanatory power.

The surrounding matrix is a source of bird species in a fynbos patch not typically found in fynbos habitat (Wethered & Lawes 2005; Litteral & Wu 2012). Each of these non-fynbos matrix habitats have generalist species, and some also have their own cohort of habitat specialists, which occasionally cross into the fynbos habitat of the study patches (Wethered & Lawes 2005; Litteral & Wu 2012). Some species only traverse across the patch, while others may make use of resources e.g. nectar or prey, although it is not their typical habitat (Poulin & Villard 2011; Driscoll et al. 2013). In the smaller patches point-count locations were per force positioned closer to the edge than in the medium and especially large patches, where I generally had options to place them further from edge habitat. The closer a point-count is located to the patch edge, the more likely you are to encounter non-fynbos species and species that only occasionally use fynbos from the surrounding matrix (Ewers et al. 2007; Sandberg et al. 2016).

Patch size was also correlated with available fynbos habitat around a patch in the study. It is thus more likely that a larger patch will have suitable fynbos habitat for fynbos endemics and other birds associated with fynbos around the point-counts. Species richness was influenced by the surrounding non-fynbos habitat matrix in combination with patch size with a high proportion of non-fynbos typical species recorded in the smaller patches and the converse in larger patches (see Chapter 2, methods; Table 2.1, Figure 3.2 and Table 3.4) (Kennedy et al. 2010; Neuschulz et al. 2011; Öckinger et al. 2012a, 2012b; Driscoll et al. 2013; Fahrig 2013). Similar findings are, for instance, reflected in a study in Brazil that investigated differences in bird community composition in 31 patches of fragmented and intact Atlantic forest (Banks-Leite et al. 2010). The influence of the surrounding non-Atlantic forest habitat matrix resulted in fewer forest specialist and insectivorous bird species and more non-forest specialist hummingbirds at the edges of the large and medium patches and throughout smaller patches (Banks-Leite et al. 2010). In contrast, the bird community composition at the center of large patches was similar to those in intact forest (Banks-Leite et al. 2010).

Although it was unclear if fragmentation had a negative effect on fynbos bird species richness, evidence from literature in this well-studied field suggests that fragmentation likely has a negative effect on fynbos bird species richness (Pauw & Louw 2012; Sandberg et al. 2016; Geerts et al. 2020). Habitat specialists are generally negatively affected by aspects of fragmentation including from the influence of the surrounding matrix through edge effects, competition from non-habitat typical species that make use of the same resources and non-habitat typical predators that penetrate the remaining habitat (Banks-Leite et al. 2010; Poulin & Villard 2011). For example, in a study in fynbos habitat in Knysna, South Africa, the proportion of fynbos-typical and fynbos non-typical bird species in fragmented patches differed significantly from large unfragmented fynbos areas (Sandberg et al. 2016). There was a marked under-representation of fynbos typical and specialist species and an over-representation of fynbos non-typical species in the fragmented patches (Sandberg et al. 2016). These patterns reflected the nature of the surrounding matrix where generalist, farm, exotic tree plantation and forest typical species were over-represented in fragmented patches (Sandberg et al. 2016).

It is essential to consider a species' characteristics and habitat preferences when interpreting the impacts of fragmentation (Pfeifer et al. 2017; Betts et al. 2019). Habitat specialists, for instance, are less likely to move into or over surrounding matrix habitat types than generalist species (Antongiovanni & Metzger 2005; Vetter et al. 2011). For example, in Afromontane forest in Taita Hills, Kenya, generalist White-starred Robins (*Pogonocichla stellata*), were less selective over which matrix types they moved between among fragmented Afromontane patches, whereas the forest specialist Cabanis's Greenbul (*Phyllastrephus cabanisi*) selected matrix types similar to the forest habitat i.e. woodland to move between patches (Aben et al. 2012). Researchers also demonstrated in an experimental study at the Las Cruces Biological Station, Costa Rica, that forest specialist hummingbirds were less likely to use resources in the non-forest matrix than habitat generalist hummingbirds (Kormann et al. 2016). The results of all four analyses in my study that considered nectarivore abundance support that the different species' characteristics determine how the available fynbos habitat, patch size, and surrounding matrix influence where they are most abundant. A study in Cape Town, South Africa, that examined some of the same species, showed that bird nectarivores reacted differently to urban environments. Southern Double-collared Sunbirds ventured farthest into urban environments and occurred throughout the urban gradient, whereas Malachite Sunbirds tended to stay within 1 km of fynbos habitat, and Orange-breasted Sunbirds and Cape Sugarbirds did not penetrate into urban environments at all, indicating that they are likely more sensitive to urbanisation (Pauw & Louw 2012). The authors concluded that these differences among species result from their specific characteristics and habitat and resource requirements (Pauw & Louw 2012).

For each of the six nectarivores in my study, the amount of fynbos habitat surrounding a point-count, and thus patch size, was either a positive or negative driver (or suggested as such). The nectarivore abundance analyses showed that fragmentation negatively impacted fynbos specialist bird species. Both endemic nectarivores, Cape Sugarbird and Orange-breasted Sunbird, were negatively associated with the loss of fynbos habitat associated with the smaller patches. I could not demonstrate whether there are lower size and/or isolation thresholds below which Cape Sugarbirds and Orange-breasted Sunbirds are unlikely to persist in a patch. Cape Sugarbirds are known to move long-distances, increasing their chances of encountering isolated habitat patches (Fraser 1997). They might thus still find and visit small patches, even if they have only a few proteas (Altwegg & Underhill 2006). Orange-breasted Sunbirds more clearly suggest a lower patch-size threshold because they occurred at low abundances or were even absent from the smallest patches. I could though not statistically test for such a threshold as I did not have enough sites and did not collect enough data, especially for the smaller sites. Both fynbos endemic nectarivores also showed the expected strong association with an increase in fynbos habitat and the plant species they feed on and pollinate. Cape Sugarbirds associated with an increase in proteas and Orange-breasted Sunbirds with ericas (Brown 2005a, 2005b; Geerts 2011; Schmid et al. 2016). Cape Sugarbird are strongly associated with intact fynbos with an abundance of proteas for nectar, insects and nesting (Daniels et al. 2001; Brown 2005a; Schmid et al. 2016). Outside of the breeding season, Cape Sugarbird make use of other nectar sources but their movement patterns are closely associated with protea flowering (Schmid et al. 2016) (see also chapter 4).

Southern Double-collared Sunbirds are generalist feeders that make use of a wide variety of habitats and vegetation growth forms including fynbos (Smith & Tree 2005). They have an expanded niche in the west of their range, and become increasingly specialised as they encounter more competing sunbirds towards the east of their range (Cody 1983). The results point towards their generalist feeding nature with a suggested negative association with fynbos habitat. This is in contrast to the similar sized, Orange-breasted Sunbird that is negatively affected by a decrease in fynbos habitat, and thus, in the context of the study, patch size and fragmentation. Southern Double-collared Sunbirds might benefit from fragmentation, at the expense of Orange-breasted Sunbirds. The constraints of fragmentation on Orange-breasted Sunbirds in smaller-sized patches might even lead to hybridisation with Southern Double-collared Sunbirds (Ryan 2020). In addition to the ericas and other nectar sources in the fynbos, Southern Double-collared Sunbirds take advantage of a variety of habitats and food sources in the diversity of surrounding matrices which allows for them to occur at higher densities in smaller patches. Another factor that may play a role in the negative association of Southern Double-collared Sunbirds with patch size is the potential, but unexplored impacts of competition and potential dominance of Orange-breasted Sunbirds over South Double-collared Sunbirds in larger-sized fynbos patches where the former occurs in higher densities (Cody 1983). This relationship might change as fynbos ages and matures post fire and Southern Double-collared Sunbirds penetrate further into it (P.G. Ryan, University of Cape Town, pers. comm.). Malachite Sunbirds seemed to be negatively affected by fragmentation and/or positively associated with patch size. They are not fynbos specialists, but they are typical of fynbos and are associated with large intact swathes of suitable habitat including in fynbos (Brown 2005c). They are though only likely to be found if they have access to abundant long-tubed flowering plants, including proteas, that satisfy their higher nectar requirement (Geerts and Pauw 2009b). Malachite Sunbirds, for instance, make use of the abundant bird pollinated Tree Fuchsia (*Halleria lucida*) found in many of the remnant farmland and riverine sections in the surrounding matrix (personal observation). Both the Amethyst and Greater Double-collared Sunbirds, like the Southern Double-collared Sunbird, also showed that they would likely benefit from the fragmentation of fynbos habitat and the increased diversity of habitats and food sources from the surrounding matrix.

Conclusions

In this chapter I aimed to establish if and how fynbos fragmentation affects bird species richness and nectarivore presence. Patch size in combination with the surrounding non-fynbos habitat matrix composition influenced bird communities and individual species abundance. Smaller-sized patches, that had more influence from the surrounding matrix habitat, had higher species richness. Habitat specialist bird nectarivores reacted negatively and habitat generalists positively to habitat fragmentation. The findings generally support that it is worth being precautionary and to consider conserving remaining fynbos habitat, even if only small patches remain. As long as you have intact fynbos, the likelihood is there that the specialist bird species that pollinate the fynbos plants will still visit to feed on and pollinate those species even if they only use the patches as stepping stones to larger habitat patches (Aben et al. 2012). All parties with intact fynbos under their care should aim to protect the habitat against further habitat loss and fragmentation. Where possible, land managers and conservers should attempt to increase connectivity between patches by removing alien vegetation within and between patches. Such cleared areas, if kept invasive-species free, will gradually revert to fynbos habitat, and this process can be enhanced by active rehabilitation (Roura-Pascual et al. 2009; van Wilgen 2009).

Appendices

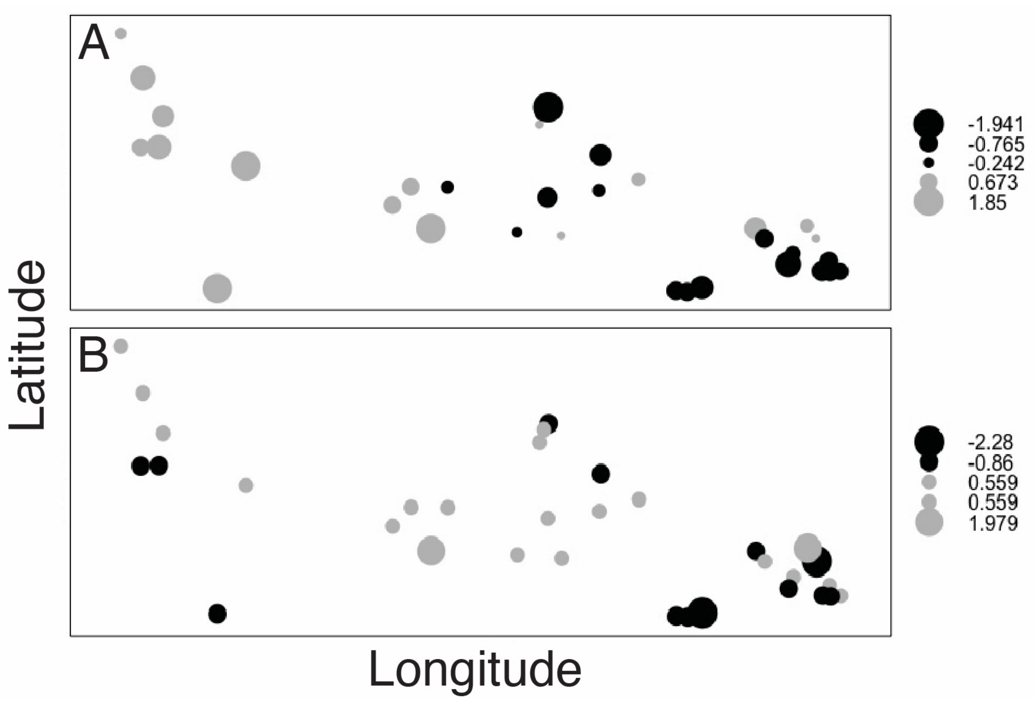
Appendix 3.1: List of avifauna species recorded in this study during point-counts. Foraging style: AR – on the wing; TR – close or on the surface; AQ – close or on the water. Feeding guild: CA - carnivore; FR – frugivore; GN – generalist; GR – granivore; IN – insectivore; NE – nectarivore. Nectar usage: 0 - no usage; 1 - occasional usage; 2 – abundant usage; 3 – obligate nectarivore. Fynbos status: E – fynbos endemic; NE – near endemic; N – not endemic; A – alien from outside southern-Africa. Fynbos typical: species commonly seen (Y) or not (N) when moving around in the fynbos of the study area. Fynbos usage: MU – much usage; SU – some usage; PU – peripheral (seldom) usage; NU – no usage. The list is sorted by obligate/abundant nectar usage, fynbos status, fynbos typical and then fynbos usage classification.

Common name	Scientific name	Point-count(s)			Foraging style	Feeding guild	Nectar usage	Fynbos		
		recorded	records	counts				Status	Typical	Usage
Cape Sugarbird	*Promerops cafer*	88	422	858	TR	NE	3	E	Y	MU
Orange-breasted Sunbird	*Anthobaphes violacea*	98	403	482	TR	NE	3	E	Y	MU
Southern Double-collared Sunbird	*Cinnyris chalybeus*	129	478	558	TR	NE	3	N	Y	MU
Greater Double-collared Sunbird	*Cinnyris afer*	70	112	132	TR	NE	3	N	Y	SU
Malachite Sunbird	*Nectarinia famosa*	47	136	147	TR	NE	3	N	Y	SU
Amethyst Sunbird	*Chalcomitra amethystina*	81	137	173	TR	NE	3	N	N	SU
Collared Sunbird	*Hedydipna collaris*	3	3	4	TR	IN	3	N	N	NU
Grey Sunbird	*Cyanomitra veroxii*	4	4	4	TR	NE	3	N	N	NU
Cape Weaver	*Ploceus capensis*	8	10	31	TR	IN	2	N	Y	SU
Cape White-eye	*Zosterops virens*	100	162	1020	TR	GN	2	N	Y	SU
Cape Siskin	*Crithagra totta*	18	29	56	TR	GR	1	E	Y	MU
Victorin's Warbler	*Cryptillas victorini*	105	337	353	TR	IN	0	E	Y	MU
Cape Bulbul	*Pycnonotus capensis*	21	23	27	TR	FR	1	NE	Y	MU
Cape Canary	*Serinus canicollis*	3	3	5	TR	GR	0	N	Y	MU
Cape Grassbird	*Sphenoeacus afer*	54	111	117	TR	IN	0	N	Y	MU
Cape Robin-chat	*Cossypha caffra*	89	156	163	TR	IN	0	N	Y	MU
Karoo Prinia	*Prinia maculosa*	89	283	353	TR	IN	0	N	Y	MU
Brimstone Canary	*Crithagra sulphurata*	57	73	132	TR	GR	1	N	Y	SU
Neddicky	*Cisticola fulvicapilla*	22	27	28	TR	IN	1	N	Y	SU
Streaky-headed Seedeater	*Crithagra gularis*	2	3	3	TR	GR	1	N	Y	SU
Bar-throated Apalis	*Apalis thoracica*	51	76	101	TR	IN	0	N	Y	SU
Common Waxbill	*Estrilda astrild*	4	4	12	TR	GR	0	N	Y	SU
Forest Canary	*Crithagra scotops*	11	13	20	TR	GR	0	N	Y	SU
Grey-backed Cisticola	*Cisticola subruficapilla*	3	5	6	TR	IN	0	N	Y	SU
Jackal Buzzard	*Buteo rufofuscus*	1	1	1	TR	CA	0	N	Y	SU
Red-necked Spurfowl	*Pternistis afer*	22	28	36	TR	GN	0	N	Y	SU
Yellow Bishop	*Euplectes capensis*	13	18	35	TR	GR	0	N	Y	SU
Black-winged Kite	*Elanus caeruleus*	1	1	2	TR	CA	0	N	N	PU
Cape Crow	*Corvus capensis*	6	6	6	TR	CA	0	N	N	PU
Ring-necked Dove	*Streptopelia capicola*	57	83	106	TR	GR	0	N	N	PU
Southern Boubou	*Laniarius ferrugineus*	113	254	392	TR	IN	0	N	N	PU
Southern Fiscal	*Lanius collaris*	15	17	18	TR	IN	0	N	N	PU
Swee Waxbill	*Coccopygia melanotis*	2	2	16	TR	GR	0	N	N	PU
African Black Swift	*Apus barbatus*	14	18	166	AR	IN	0	N	N	PU
Alpine Swift	*Tachymarptis melba*	1	1	10	AR	IN	0	N	N	PU
Barn Swallow	*Hirundo rustica*	15	20	121	AR	IN	0	N	N	PU
Cape Wagtail	*Motacilla capensis*	2	2	2	TR	IN	0	N	N	PU
Greater Striped Swallow	*Cecropis cucullata*	17	22	97	AR	IN	0	N	N	PU
Knysna Woodpecker	*Campethera notata*	10	13	13	TR	IN	0	N	N	PU
Lanner Falcon	*Falco biarmicus*	1	1	1	TR	CA	0	N	N	PU
Lazy Cisticola	*Cisticola aberrans*	22	30	33	TR	IN	0	N	N	PU
Olive Woodpecker	*Dendropicos griseocephalus*	17	18	18	TR	IN	0	N	N	PU
Southern Tchagra	*Tchagra tchagra*	2	2	2	TR	IN	0	N	N	PU
White-rumped Swift	*Apus caffer*	1	1	10	AR	IN	0	N	N	PU
Black-bellied Starling	*Notopholia corrusca*	1	1	3	TR	GN	1	N	N	NU
Black-headed Oriole	*Oriolus larvatus*	67	84	93	TR	IN	1	N	N	NU
Fork-tailed Drongo	*Dicrurus adsimilis*	34	48	64	TR	IN	1	N	N	NU
Red-winged Starling	*Onychognathus morio*	23	35	80	TR	GN	1	N	N	NU
Terrestrial Brownbul	*Phyllastrephus terrestris*	3	3	5	TR	IN	1	N	N	NU
African Dusky Flycatcher	*Muscicapa adusta*	2	2	2	TR	IN	0	N	N	NU
African Emerald Cuckoo	*Chrysococcyx cupreus*	3	6	7	TR	IN	0	N	N	NU
African Hoopoe	*Upupa africana*	1	1	1	TR	IN	0	N	N	NU
African Olive Pigeon	*Columba arquatrix*	4	4	29	TR	FR	0	N	N	NU

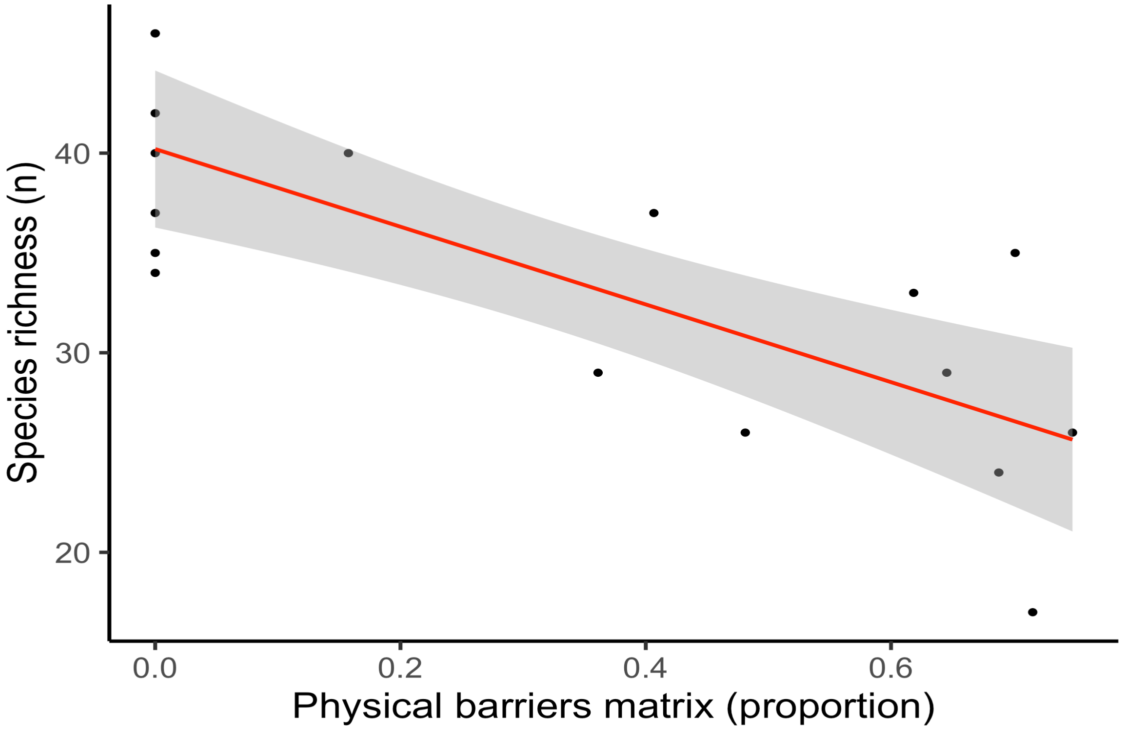
Common name	Scientific name	Point-count(s) recorded	Point-count(s) records	Point-count(s) counts	Foraging style	Feeding guild	Nectar usage	Fynbos Status	Fynbos Typical	Fynbos Usage
African Oystercatcher	*Haematopus moquini*	1	1	3	AQ	CA	0	N	N	NU
African Paradise Flycatcher	*Terpsiphone viridis*	3	3	4	TR	IN	0	N	N	NU
Black Cuckooshrike	*Campephaga flava*	9	9	9	TR	IN	0	N	N	NU
Black Saw-wing	*Psalidoprocne pristoptera*	8	13	46	AR	IN	0	N	N	NU
Black-backed Puffback	*Dryoscopus cubla*	1	1	1	TR	IN	0	N	N	NU
Black-headed Heron	*Ardea melanocephala*	1	1	1	AQ	CA	0	N	N	NU
Blacksmith Lapwing	*Vanellus armatus*	1	1	1	AQ	CA	0	N	N	NU
Blue Crane	*Grus paradisea*	1	1	3	TR	GN	0	N	N	NU
Blue-mantled Crested Flycatcher	*Trochocercus cyanomelas*	1	1	1	TR	IN	0	N	N	NU
Brown-hooded Kingfisher	*Halcyon albiventris*	4	4	4	TR	IN	0	N	N	NU
Burchell's Coucal	*Centropus burchellii*	8	8	11	TR	CA	0	N	N	NU
Cape Batis	*Batis capensis*	25	29	38	TR	IN	0	N	N	NU
Cape Cormorant	*Phalacrocorax capensis*	2	3	6	AQ	CA	0	N	N	NU
Chorister Robin-chat	*Cossypha dichroa*	1	1	1	TR	IN	0	N	N	NU
Crowned Eagle	*Stephanoaetus coronatus*	1	1	1	TR	CA	0	N	N	NU
Egyptian Goose	*Alopochen aegyptiaca*	25	26	40	AQ	GR	0	N	N	NU
Forest Buzzard	*Buteo trizonatus*	6	6	7	TR	CA	0	N	N	NU
Green Wood Hoopoe	*Phoeniculus purpureus*	12	12	19	TR	IN	0	N	N	NU
Green-backed Camaroptera	*Camaroptera brachyura*	7	8	8	TR	IN	0	N	N	NU
Grey Cuckooshrike	*Ceblepyris caesius*	3	3	5	TR	IN	0	N	N	NU
Hadada Ibis	*Bostrychia hagedash*	46	55	86	TR	IN	0	N	N	NU
Helmeted Guineafowl	*Numida meleagris*	6	7	7	TR	GN	0	N	N	NU
Kelp Gull	*Larus dominicanus*	7	9	13	AQ	CA	0	N	N	NU
Klaas's Cuckoo	*Chrysococcyx klaas*	5	5	5	TR	IN	0	N	N	NU
Knysna Turaco	*Tauraco corythaix*	23	29	33	TR	FR	0	N	N	NU
Lemon Dove	*Columba larvata*	1	1	1	TR	GR	0	N	N	NU
Olive Bushshrike	*Chlorophoneus olivaceus*	8	8	8	TR	IN	0	N	N	NU
Pied Crow	*Corvus albus*	1	1	1	TR	CA	0	N	N	NU
Red-chested Cuckoo	*Cuculus solitarius*	20	23	25	TR	IN	0	N	N	NU
Red-eyed Dove	*Streptopelia semitorquata*	27	29	32	TR	GR	0	N	N	NU
Scaly-throated Honeyguide	*Indicator variegatus*	2	2	2	TR	IN	0	N	N	NU
Sombre Greenbul	*Andropadus importunus*	91	176	203	TR	FR	0	N	N	NU
Southern Grey-headed Sparrow	*Passer diffusus*	3	3	3	TR	GR	0	N	N	NU
Speckled Mousebird	*Colius striatus*	10	10	26	TR	FR	0	N	N	NU
Speckled Pigeon	*Columba guinea*	3	3	3	TR	GR	0	N	N	NU
White-breasted Cormorant	*Phalacrocorax lucidus*	1	1	1	AQ	CA	0	N	N	NU
White-necked Raven	*Corvus albicollis*	24	24	31	TR	CA	0	N	N	NU

Appendix 3.2: List of additional avifauna species recorded incidentally while moving through the patches during fieldwork.

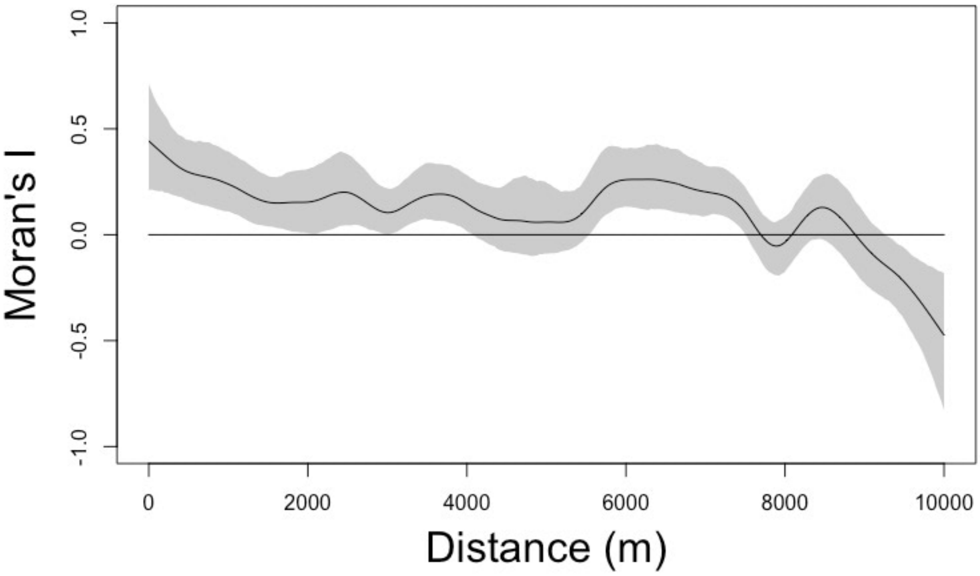
Common name	**Scientific name**
Cape Spurfowl	*Pternistis capensis*
African Fish Eagle	*Haliaeetus vocifer*
African Goshawk	*Accipiter tachiro*
African Sacred Ibis	*Threskiornis aethiopicus*
African Spoonbill	*Platalea alba*
Black Sparrowhawk	*Accipiter melanoleucus*
Common Quail	*Coturnix coturnix*
Common Starling	*Sturnus vulgaris*
Crowned Lapwing	*Vanellus coronatus*
Diederik Cuckoo	*Chrysococcyx caprius*
Fiery-necked Nightjar	*Caprimulgus pectoralis*
Golden-breasted Bunting	*Emberiza flaviventris*
Greater Crested Tern	*Thalasseus bergii*
Greater Honeyguide	*Indicator indicator*
Long-crested Eagle	*Lophaetus occipitalis*
Narina Trogon	*Apaloderma narina*
Olive Thrush	*Turdus olivaceus*
Pin-tailed Whydah	*Vidua macroura*
Reed Cormorant	*Microcarbo africanus*
Rock Martin	*Ptyonoprogne fuligula*
Rufous-breasted Sparrowhawk	*Accipiter rufiventris*
White Stork	*Ciconia ciconia*
Yellow-billed Duck	*Anas undulata*
Yellow-billed Kite	*Milvus aegyptius*
Cape Rock Thrush	*Monticola rupestris*
Fiscal Flycatcher	*Melaenornis silens*
African Stonechat	*Saxicola torquatus*
Booted Eagle	*Hieraaetus pennatus*
Cape Bunting	*Emberiza capensis*
Common House Martin	*Delichon urbicum*
White-throated Swallow	*Hirundo albigularis*



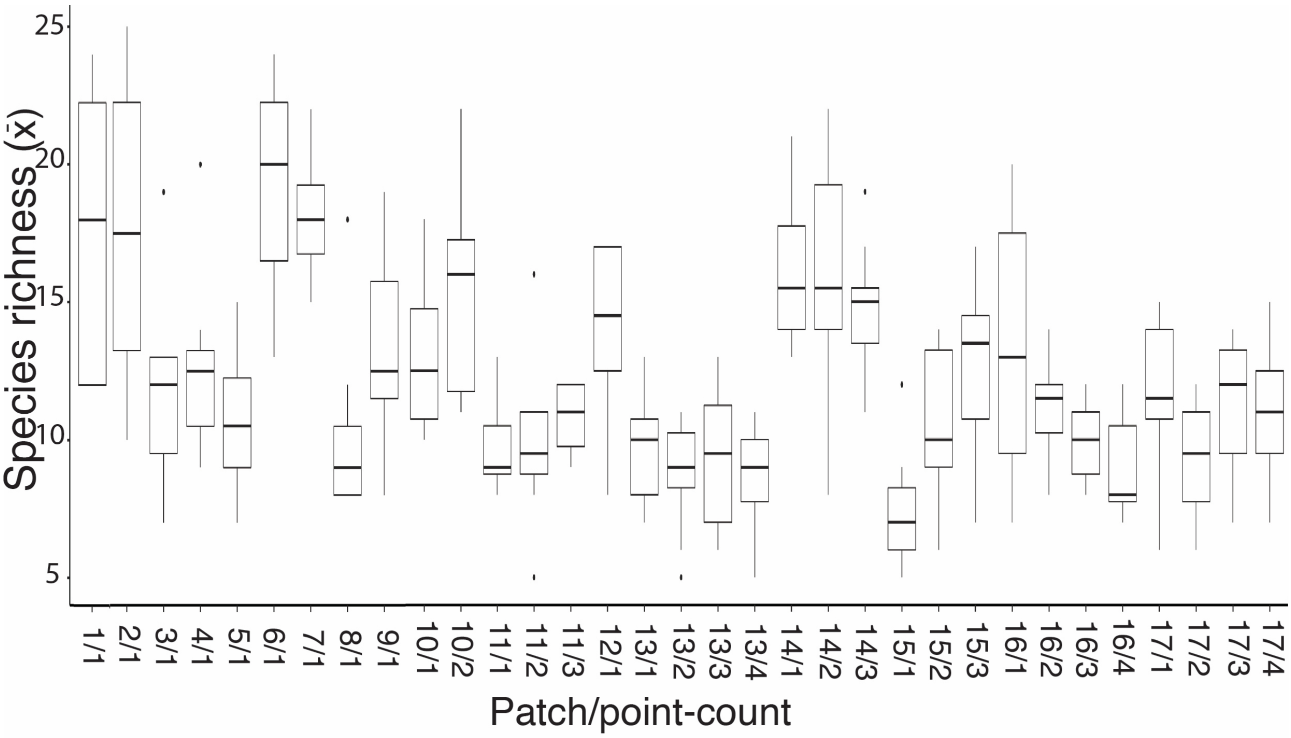
Appendix 3.3: Spatial autocorrelation for total species richness (A) and nectarivore species richness (B) for 33 point-counts located in 17 fynbos patches in the southern Cape coast of the CFR. Large circles (-1 > r > 1) indicate strong autocorrelation between counts.



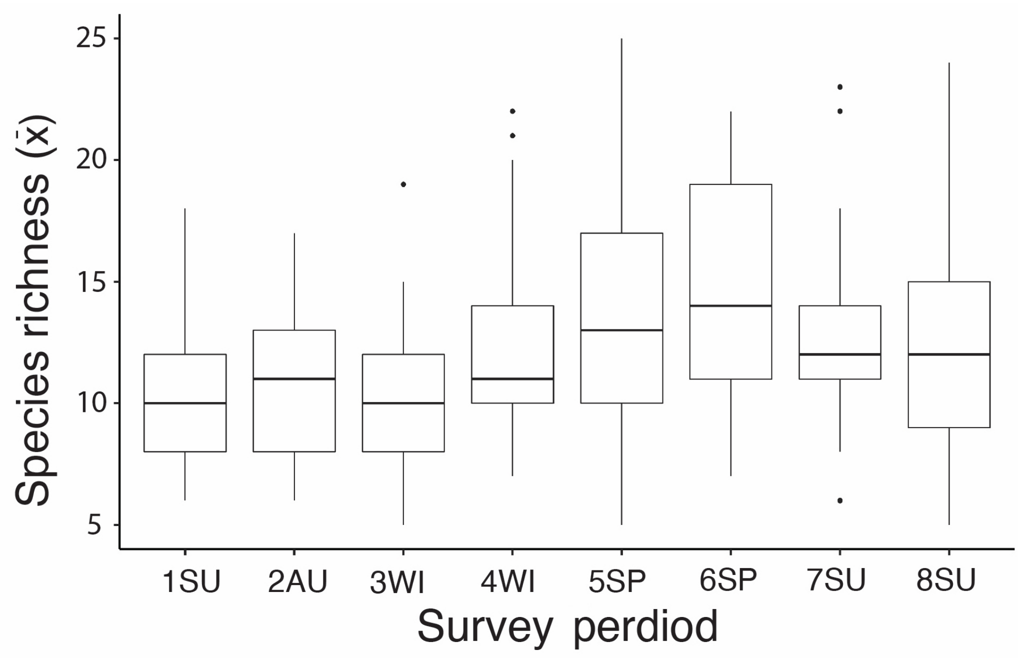
Appendix 3.4: Relationship between species richness in the study patches and the proportion of patch perimeter that is physical barrier matrix. The best fit line and standard error bands are displayed.



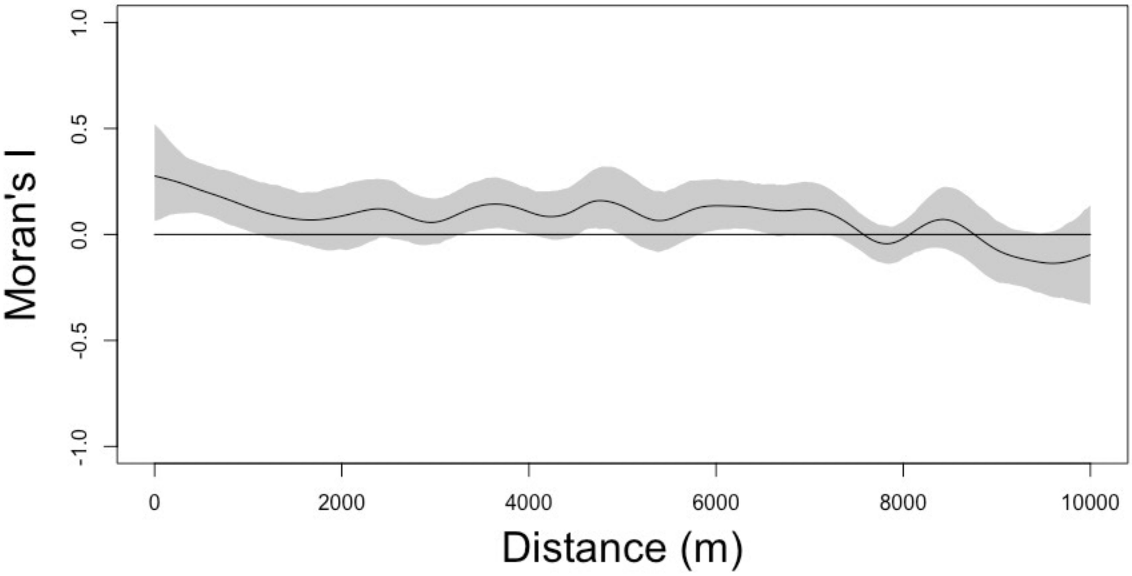
Appendix 3.5: A spline correlogram showing spatial autocorrelation in species richness between point-counts.



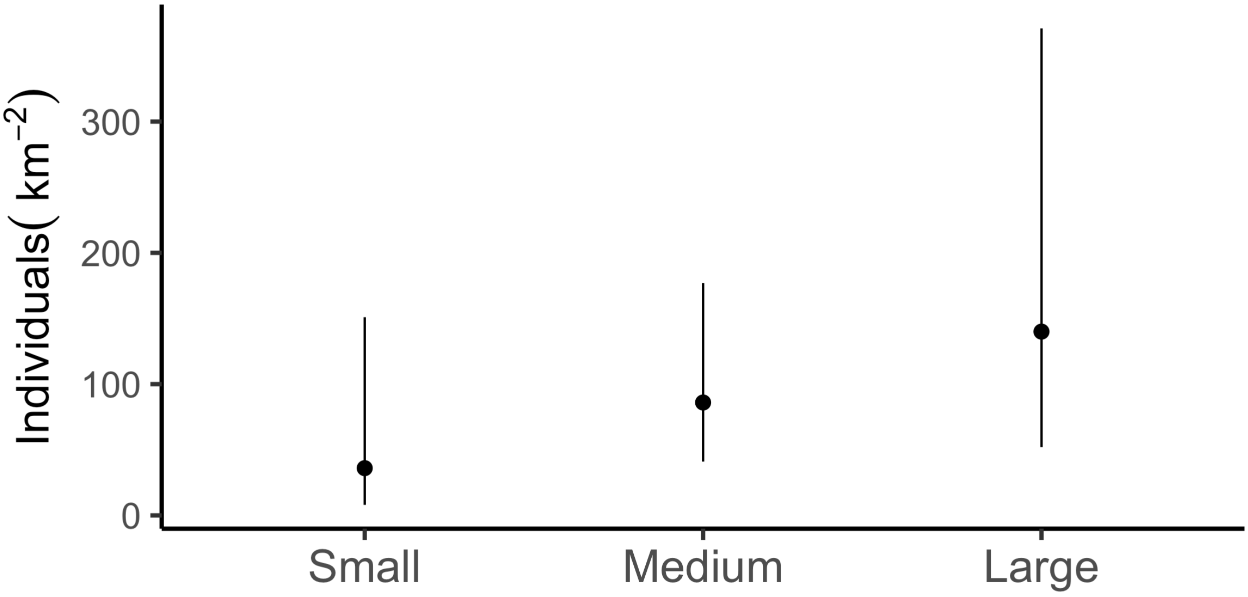
Appendix 3.6: A box plot (black line with the minimum value, a box with the first quartile, median and third quartile, and the maximum value) showing species richness for the 33 point-counts in the 17 study patches. Each count location is labelled by the patch number followed by the count replicate within that patch (see Figures 2.2 and 3.1).



Appendix 3.7: A Box plot (black line with the minimum value, a box with the first quartile, median and third quartile, and the maximum value) of species richness for the 33 point-counts in the 17 study patches between the eight survey periods.



Appendix 3.8: A spline correlogram showing spatial autocorrelation detected in Amethyst Sunbird probability of occurrence between point-counts.



Appendix 3.9: Orange-breasted Sunbird density (individuals·km^{-2}) by patch size category. Vertical lines represent confidence levels.

Chapter 4: Variation in bird-nectar relationships in a fragmented landscape in the Cape Floristic Region

Abstract

Nectar feeding birds rely on an adequate and reliable nectar supply to persist and/or breed in an area. Habitat loss and fragmentation, by reducing flowering plant abundance, has the potential to progressively affect nectar availability. In the fynbos vegetation of the Cape Floristic Region (CFR) of South Africa, a small cohort of nectar feeding bird species pollinate a large diversity of plants. The key avian pollinators in fynbos are the Cape Sugarbird (*Promerops cafer*) for proteas and the Orange-breasted Sunbird (*Anthobaphes violacea*) for ericas. This study took place in fragmented fynbos habitat in the western Tsitsikamma in the eastern region of the CFR. I investigated if habitat fragmentation influenced nectar loads for selected protea (*Protea neriifolia* and *P. mundii*) and erica (*Erica discolor* and *E. densifolia*) flowers through its effect on the abundance of nectar-feeding birds that feed on these plants. I further investigated the phenology of protea flowering, erica and protea nectar availability, and the abundance of birds that feed on these plants. Nectar volumes per flower were lower in large patches, possibly because of higher nectarivore densities and utilisation, but there were no differences in nectar volumes per flower between small and medium patches, indicating no marked fragmentation effect in the smaller patches. However, total nectar availability per unit area was greater in large- than medium-sized patches for proteas and the opposite for ericas, which might reflect structural differences. The increase in erica nectar availability with decreasing patch was not correlated with Orange-breasted Sunbird abundance but was correlated with an increase in Southern Double-collared Sunbirds (*Cinnyris chalybeus*). Cape Sugarbirds also showed a significant positive relationship with protea nectar availability per patch, which was greater in larger patches. The number of protea flowers, the amount of nectar available and the number of Cape Sugarbirds per month were strongly correlated. These findings show the importance of nectar availability in determining nectarivore bird abundance and how fragmentation can affect it between patches.

Introduction

Birds that primarily feed on nectar can only establish territories, build nests and breed successfully in an area if sufficient nectar is produced to support them (Schmid et al. 2016). Nectar availability fluctuates depending on when and where the dominant nectar-producing plants flower (Carlson et al. 2011). Many bird species that depend on nectar resources move to track nectar across a region to fulfil their needs and requirements (Calf et al. 2003b; Altwegg & Underhill 2006). In the fynbos vegetation of the Cape Floristic Region (CFR), only 3% of bird species (nine of 323) are nectar-feeding specialists (Whelan et al. 2008). This translates to around 35 plant species dependent on each nectar-feeding species for pollination (Rebelo 1987; Aizen & Ezcurra 1998; Geerts 2011). The Cape Sugarbird (*Promerops cafer*) and Orange-breasted Sunbird (*Anthobaphes violacea*), both fynbos endemics, are not the only pollinators in the CFR, but they are key pollinators of bird-pollinated proteas and ericas, respectively (Geerts 2011; Geerts et al. 2020). Proteas provide Cape Sugarbirds with nectar and invertebrates, and are also preferred nesting species (Broekhuysen 1959; Tjørve et al. 2005; Tjørve 2007). Similarly, ericas and the fynbos habitat in which they occur provide especially Orange-breasted Sunbirds, but also Southern Double-collared Sunbirds (*Cinnyris chalybeus*), with their dietary and nesting needs (Coetzee et al. 2020; Angoh et al. 2021). The specific protea and erica species pollinated vary across the CFR depending on what species are locally available as linked to the high gamma diversity characteristics of the region (Geerts 2011; Manning & Goldblatt 2012; Ellis et al. 2014).

With bird-pollinated plants in the CFR dependent on such a small cohort of nectar-feeding birds for pollination, disturbance to the relationship can be detrimental to the long-term survival of plant species (Angoh et al. 2021). One of the main long-term environmental threats in the CFR, habitat loss and fragmentation, has the potential to affect flower nectar production and availability in an area and can even alter flowering phenology (Rouget et al. 2003b; Xiao et al. 2016). In this chapter I investigate how nectar availability of selected protea (*Protea neriifolia* and *P. mundii*) and erica (*Erica discolor* and *E. densifolia*) species differs between fynbos patches in fragmented fynbos habitat. I focus only on a small subset of flowering plants in the area, but my assumption is that these species are major nectar sources for the bird species of interest. If birds are absent or low in abundance from smaller-sized patches because of fragmentation factors, I expect that nectar volume per flower will be higher than constant consumption volume, whilst if bird visitation is increased from the surrounding matrix, I expect nectar volume per flower to be lower (Figure 4.1). I expect larger-sized patches to have either more, or less, nectar per flower than smaller-sized patches depending on how fragmentation influences bird abundance and thus nectar consumption.

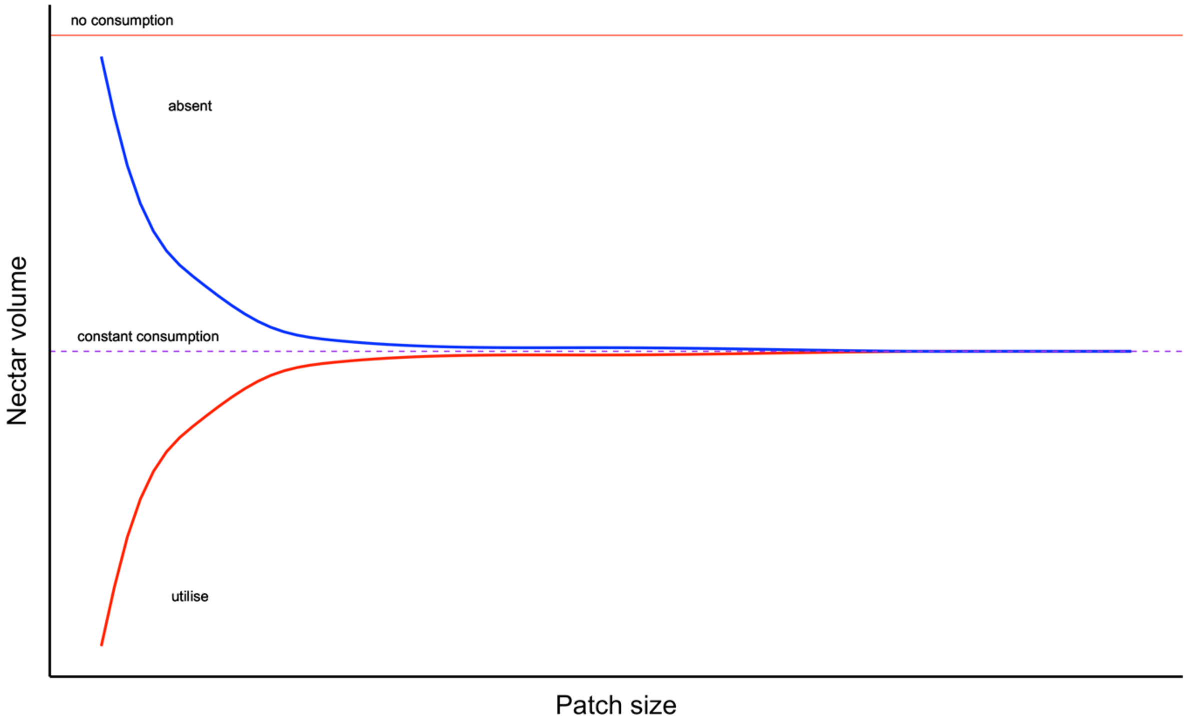


Figure 4.1: Average nectar volume per flower in small patches is predicted to be either lower than expected compared with constant consumption because of increased utilisation, for example, additional birds feeding from the surrounding non-habitat matrix (utilise); or higher (closer to no consumption bagged nectar volume) because of there being fewer or no birds to utilise the nectar (absent).

I expect that the patterns of nectar utilisation in relation to patch size will differ for proteas and ericas. Proteas are primarily fed on and pollinated by Cape Sugarbirds, whereas ericas are potentially used by several bird species other than the fynbos endemic Orange-breasted Sunbird, including Southern Double-collared Sunbirds (Brown 2005b, 2005a; Smith & Tree 2005). To establish whether nectarivory impacts nectar volume, I compare nectar volumes and concentrations between accessible flowers, and flowers where pollinators were excluded experimentally. I predict that flowers where birds were excluded will have higher nectar volumes, but nectar sugar concentrations will be similar because the latter is largely independent of nectar volume (Bartoš et al. 2012). I further assess whether plant species' nectar volume influences sunbird and sugarbird abundance in each patch. I also explore the monthly flowering phenology of protea species, as well as how the birds and protea and erica nectar relate to each other monthly across the study area. I predict that monthly protea nectar availability is positively related to protea flower abundance, and that the Cape Sugarbird, a species known to seasonally track protea flower abundance (Altwegg & Underhill 2006; Schmid et al. 2016), will relate positively to both monthly protea flower abundance and nectar availability.

Methods

Study area, patches, survey periods, point-counts and other variables

The study area in the western Tsitsikamma in the CFR comprised of 17 fynbos patches of varied sizes (Chapter 2). I undertook the fieldwork in eight approximately six-week survey periods during 2016-2017 (Table 3.1). During each survey period, I undertook 10-minute bird point-counts from set locations in each patch (Chapter 3). There were one to four locations per patch, depending on patch size (Chapter 3). I also estimated several vegetation variables during each survey period and point-counts recording the relative density of proteas and ericas, and vegetation biomass around each point-count (Chapters 2 and 3). I also conducted arial drone surveys to estimate protea densities for each patch (Chapter 2).

Bird-pollinated plant species and their associated bird species

I identified 14 common bird-pollinated fynbos plants in the study area during my initial field surveys and based on what other studies identified (Angoh et al. 2017; Whitehead 2018; Bestea et al. 2019): *Chasmanthe aethiopica, Erica densifolia, E. discolor, E. glandulosa fourcadei, E. sessiliflora, Gladiolus huttonii, Kniphofia uvaria, Leucospermum cuneiforme, Protea cynaroides, P. mundii, P. neriifolia, Tritoniopsis caffra, Watsonia fourcadei* and W. *knysnana*. I recorded the presence of these species seen during each of the eight survey visits to a patch. Only two proteas (*P. mundii* and *P. neriifolia*) and two ericas (*E. densifolia and E. discolor*) were sufficiently common, widespread, and accessible to be sampled in most patches.

Flower collection and nectar sampling

During selected field visits to a patch, I sampled nectar volumes in 10 mature (see age estimation below) and intact flowerheads of each protea species and 20 flowers of *E. discolor*. The first collection was on the first field visit during the first survey period, and then for every second field visit thereafter (third, fifth and seventh survey period). I also collected *P. neriifolia* in the eighth survey period after it did not flower from the fifth to seventh survey periods. I collected 20 *E. densifolia* flowers during any survey period that it flowered, as the species did not flower synchronously. I conducted 24-hour nectar production sampling for *P. neriifolia* and for *E. discolor* in patch 17 on 16 and 31 March 2017 (Figure 2.2). On each date from around 8 am I bagged (to exclude all pollinators) 20 open protea flowers and 30 open erica flowers for 24 hours, then collected them to record nectar amounts. I extracted nectar on the same day that I collected all flowers. Proteas have compound flowers, so I could not effectively sample nectar from individual flowers. Instead, nectar from protea flowerheads was extracted using a simple centrifuge (Armstrong & Paton 1990; Schmid et al. 2016; Nottebrock et al. 2017; Appendix 4.1). I placed a protea flowerhead in a funnel made from a two-litre plastic bottle with the lower half cut off. I then attached a sampling vial to the remaining funnel end so that I could collect any nectar extracted. To hold the vial, and funnel with the flowerhead in place, I secured a plastic bag around it. I tied a 1.5 m length of 10 mm diameter rope around the flowerhead stem to secure the bag around the flowerhead, funnel and test tube and so that I could swing it to extract the nectar (Appendix 4.1). Each flowerhead was rotated for 60 seconds at approximately 1.5 revolutions per second (Armstrong & Paton 1990). If flowerheads were wet from rain, I first hung them upside-down for three to six hours to drain the water and dry before extracting the nectar. I measured the nectar volume for proteas with a pipette for larger volumes and with 100 µl capillary tubes for smaller volumes (under 0.5 ml). For ericas I used 5 µl capillary tubes to extract and measure the nectar directly from the base of the flower tube. To measure sugar concentration, I used a hand-held refractometer (Bellingham and Stanley, Tunbridge Wells, Kent, UK: Eclipse 45–81: 0–50% sucrose w/w).

Protea florets open centripetally (from the outside in) as the flowerhead matures (Dai, Jingwei & Paull 1995; Steenhuisen et al. 2010; Zoeller et al. 2017). For each protea flowerhead I measured the length (from base to top of floral bracts to the nearest 0.1 mm using Grip 150 mm digital Vernier calliper), if there were signs of birds feeding such as displaced florets (0 – no sign, 1 – signs of feeding), and the age of the flowerhead (0 – no florets open, 1 – florets on the outside open, 2 – florets halfway to the centre open, 3 – florets to the centre open). I measured the length of each erica flower (from the base of the ovary to top of the tube to the nearest 0.01 mm), if the flower had damage (0 – no damage, 1 – damage) and if the anther ring was broken (0 – not broken, 1 – broken). A broken anther ring is an indication that a flower has been probed by a sunbird bill (Geerts & Pauw 2011). I only used damaged flowers for nectar sampling on the few occasions that there were not enough undamaged flowers collected.

Protea phenology

On the first field visit to each of the study patches I attached a durable plant tag around a branch to label 10 randomly selected individuals of both *P. neriifolia* and *P. mundii* (at the patches where they were present). The locations of each plant were recorded using a Garmin eTrex 10 GPS. During each of the eight visits to a patch, I recorded the numbers of buds, flowerheads, dried heads with seeds and old flower heads without seeds for each marked plant (Kühn et al. 2017). At the beginning of the fieldwork period (January and February 2016) there was a mismatch between the phenology monitoring and bird point-counts in some patches i.e., they fell in different months for some sites.

Data analysis

I conducted analyses in R using the RStudio development framework (R Core Team 2020; RStudio Team 2020) and the "tidyverse" collection of packages (Wickham et al. 2019). I used generalised linear models with a quasi-Poisson link function for the monthly comparisons between the number of protea flowers and protea nectar, Cape Sugarbird and protea flowers, and the focal bird species and protea/erica nectar. I also used generalised linear models with a quasi-Poisson link function to predict nectar volume, protea density/erica biomass, and nectar volume and protea density/erica biomass combined (protea/erica nectar availability), based on patch size. I combined the nectar volume (weighted by proportion of occurrence) for the two protea species, and then also for the two erica species, as that is more representative of the available nectar volume in a patch for both genera. I also used generalised linear models with a quasi-Poisson link function to investigate the relationships between sunbird and sugarbird abundance and unbagged flower nectar (on its own or combined with protea density or erica biomass).

I used linear models to see if there were differences in unbagged flower nectar volume between different patch size categories. I tested for differences among the study species over all survey periods and then also for *P. neriifolia* and *E. discolor* for each survey period that data was collected for (see Table 3.1 for survey period acronyms used). I used pairwise comparison to assess differences among patch size categories. Prior to the pairwise comparisons I first ran Kruskal Wallis chi-squared test (not reported on) to test if there were significant differences in volumes between patch size categories. I also used linear models to compare bagged and unbagged flower nectar volumes and concentrations for the selected protea and erica species. In these tests for proteas, I excluded age 3 unbagged flowers (bagged had no age 3 flowers) to compare only flowers that were producing nectar. For the erica flowers in these tests I excluded flowers not fed on (intact anther ring) in both the unbagged and bagged flowers. The convention used for boxplots are the minimum value, a box with the first quartile, median and third quartile, and the maximum value. For the unbagged flower nectar volume differences between patch size categories, I also show the raw point distribution and in red, pairwise comparison (with standard error) with same letters indicating no difference (p, 0.05).

Results

Investigating monthly protea flower, bird and nectar relationships

I found a significant positive relationship between the monthly average number of protea flowers and the monthly average combined protea flower nectar volume over the study area

(Table 4.1; Figure 4.2). Monthly average Cape Sugarbird abundance was positively related to the monthly average number of protea flowers (Table 4.1; Figure 4.3). This excludes the January and February 2016 data at the beginning of the fieldwork because of the mismatch in data collection. I did not find any relationships between monthly average Cape Sugarbird, Orange-breasted Sunbird or Southern Double-collared Sunbird abundance and monthly average protea/erica nectar volume (Table 4.1; Appendix 4.2). The monthly average abundances of Orange-breasted and Southern Double-collared Sunbirds were non-significantly related to erica nectar volume (Table 4.1; Appendix 4.3).

Table 4.1: Results of generalised linear models relating protea flowers and sugarbird and sunbird species with protea or erica nectar and/or protea flowers and/or with another sunbird species.

Flowers/birds (per month)	**Term**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Protea flowers	Intercept	-0.56	0.41	-1.37	0.21
	Protea nectar	0.74	0.21	3.44	**0.011**
Cape Sugarbird	Intercept	0.64	0.36	1.8	0.1
	Protea flowers	0.47	0.21	2.26	**0.047**
	Intercept	1.21	0.42	2.89	**0.023**
	Protea nectar	0.01	0.3	0.03	0.98
Orange-breasted Sunbird	Intercept	0.27	0.29	0.95	0.38
	Erica nectar	0.03	0.08	0.42	0.69
	Intercept	0.48	0.36	1.32	0.21
	Southern Double-collared Sunbird	0.061	0.17	0.35	0.73
Southern Double-collared Sunbird	Intercept	0.85	0.25	3.38	**0.015**
	Erica nectar	-0.06	0.07	-0.77	0.47

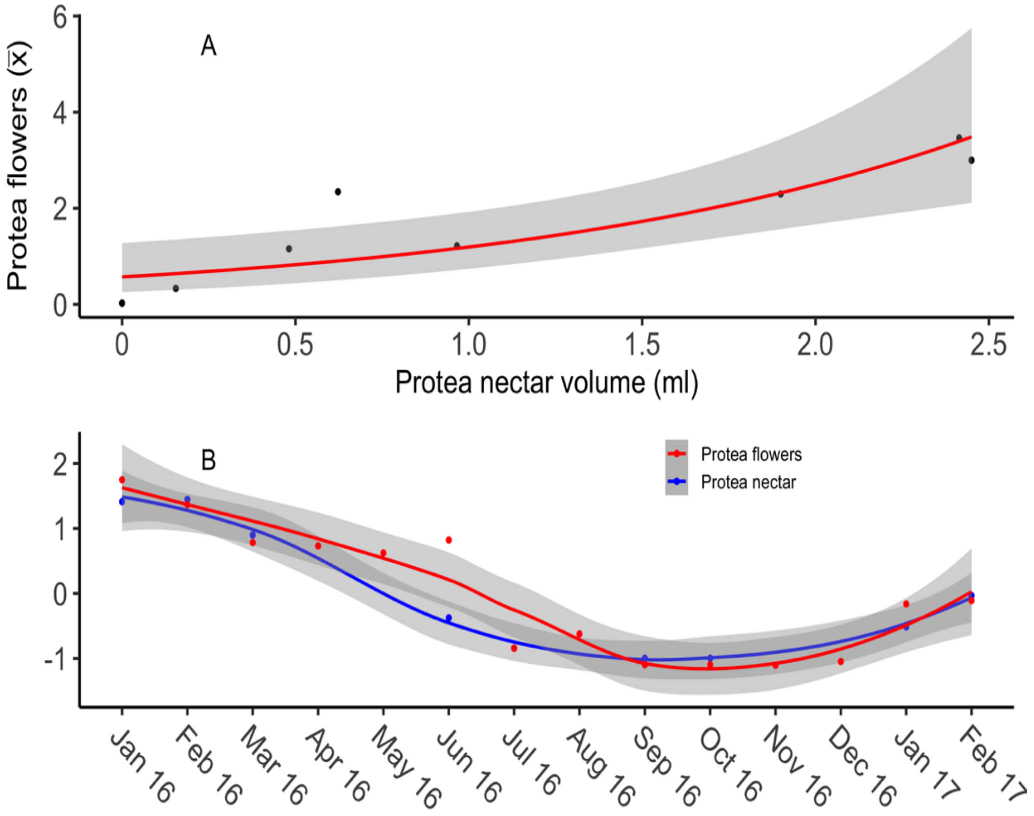


Figure 4.2: The relationship between average monthly protea flowers and average monthly protea nectar volume across the study site (A) and how each vary per month and relative to each other on the scaled graph (B). The grey shading represents the 95% confidence interval.

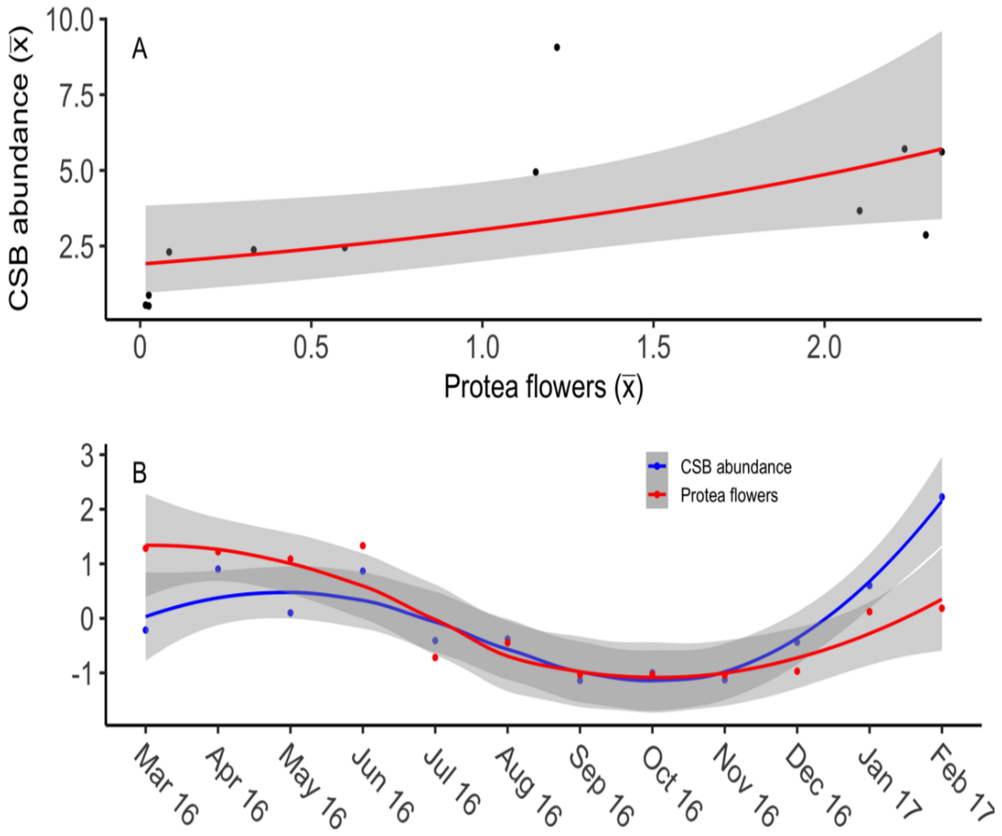


Figure 4.3: The relationship of average monthly Cape Sugarbird abundance with average monthly protea flower abundance (A). I also illustrate on the scaled graph how the relationships vary per month relative to each other (B). The grey shading represents the 95% confidence interval.

Comparing flower nectar volume among patches

The amount of nectar in *P. neriifolia* flowers was greater in medium than in large patches but not significantly so (Figure 4.4; Appendices 4.4 and 4.5). Large patches had less nectar than small and medium patches in 1SU and significantly so in 3WI (Figure 4.5; Appendices 4.4 and 4.5; refer to Table 3.1 for the meaning of the survey period abbreviations). The overall lower flower nectar volumes in 3WI (conducted in June/July 2016) compared with 1SU (conducted in January to March 2016) and the significantly lower nectar volumes in large patches can possibly be explained by *P. neriifolia* flowering being past its peak while the feeding pressure from Cape Sugarbirds was still high especially in the large patches (Figures 4.3 and 4.5; Appendices 4.4 and 4.5). Cape Sugarbirds occur in higher abundance in large patches (see Table 3.6 and Figure 3.7). In 8SU (conducted in January/February 2017), flower nectar volumes were unexpectedly higher in large patches compared with medium and significantly so with small patches (Figures 4.5; Appendices 4.4 and 4.5). This likely resulted from asynchronous flowering among patches at the beginning of the flowering period when only the large patches had mature flowers with large nectar volumes for me to collect (Figures 4.5; Appendices 4.4 and 4.5). If 8SU was excluded from the analysis, the amount of nectar in *P. neriifolia* flowers was significantly greater in medium patches than in large patches (t = 2.942, df = 228, p = 0.01). Flowers of *P. mundii* had significantly more nectar in small than in either medium or large patches (Figure 4.4, Appendix 4.4). The results for both *P. mundii* and *E. densifolia* should be considered with caution. Both species had small sample sizes as they did not occur in all patches (10 for *P. mundii* and six for *E. densifolia,* Chapter 2), flowered asynchronously among patches, and occurred in different densities and spread on the different patches. *Erica discolor* showed significantly larger nectar amounts per flower in medium than in large patches (Figure 4.4, Appendix 4.4). This pattern was also shown for each individual fieldwork survey period, but only significantly so for 5SP (Figures 4.6; Appendices 4.4 and 4.5).

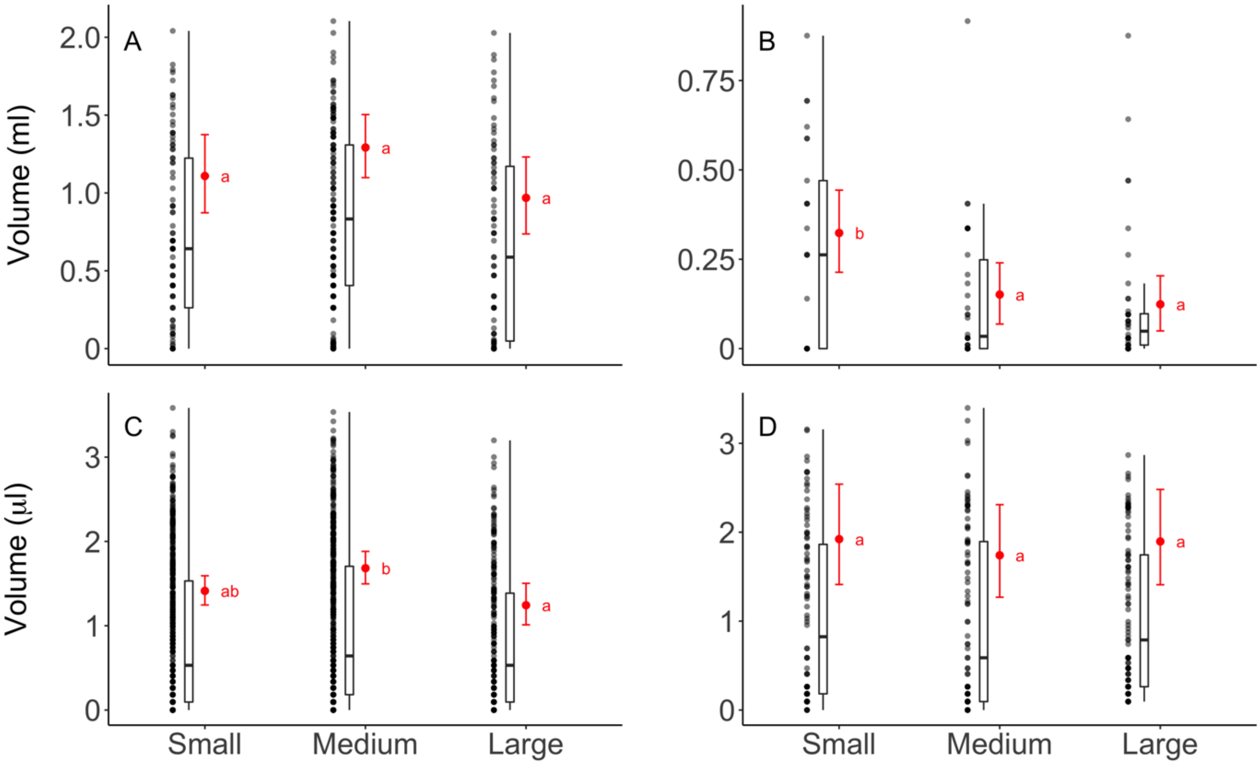


Figure 4.4: Boxplots showing the difference in flower nectar volume between patch size categories for *P. neriifolia* (A), *P. mundii* (B), *E. discolor* (C) and *E. densifolia* (D).

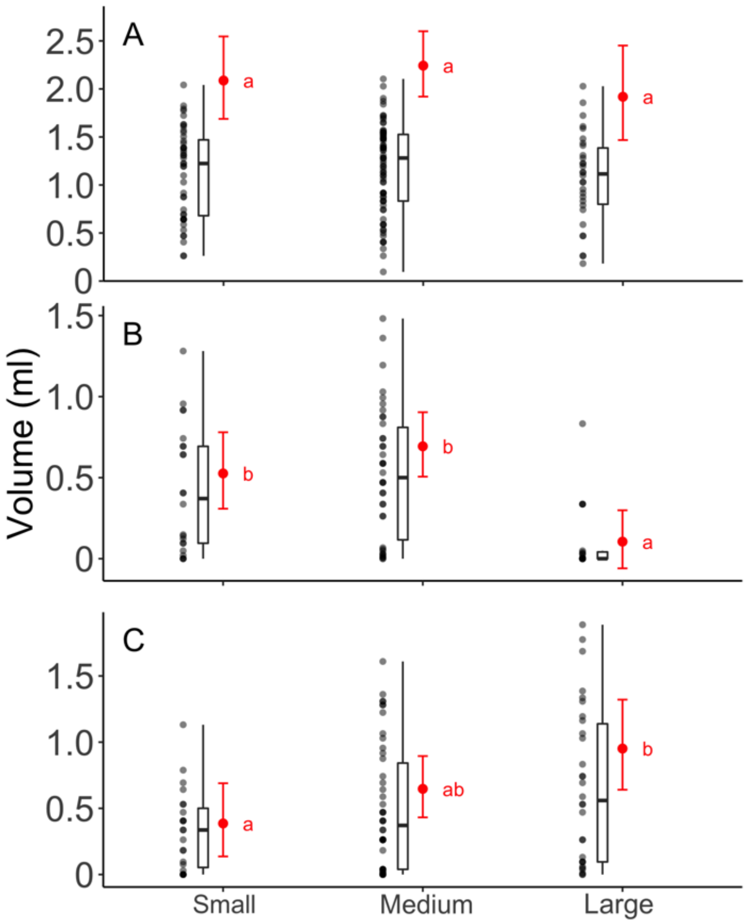


Figure 4.5: Boxplots showing the difference in *P. neriifolia* flower nectar volume between patch size categories for field survey periods 1SU (A), 3WI (B) and 8SU.

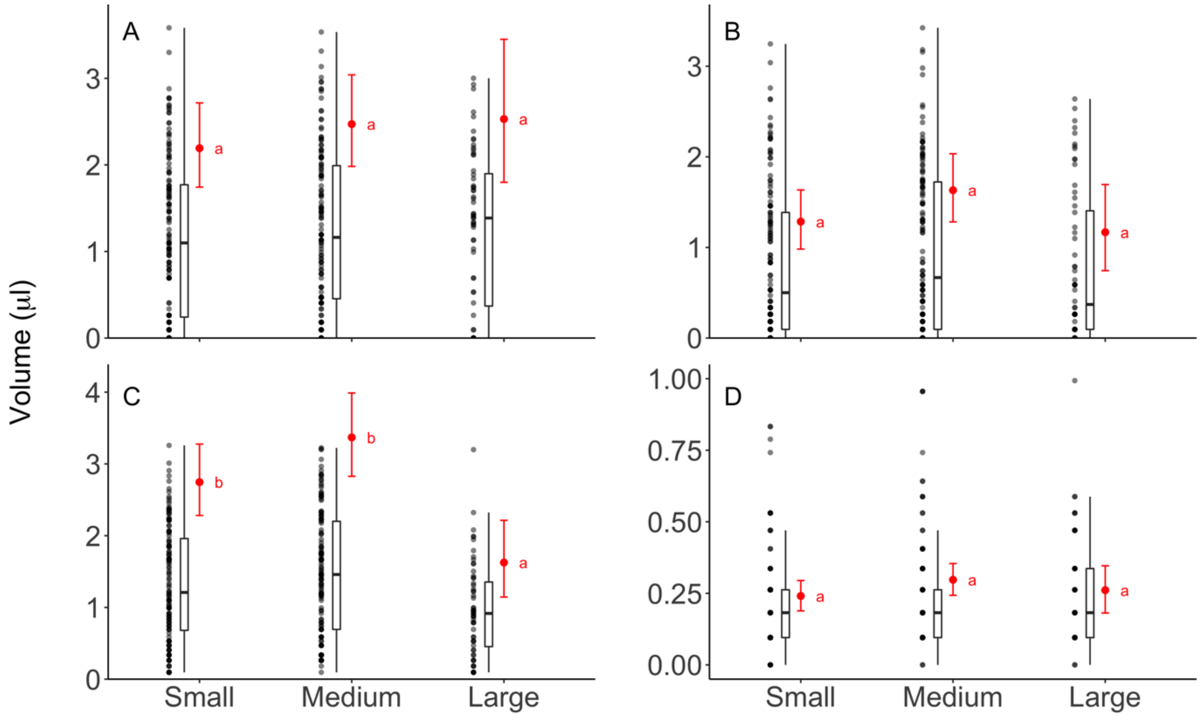


Figure 4.6: Boxplots showing the difference in *E. discolor* flower nectar volume between patch size categories for field survey periods 1SU (A), 3WI (B), 5SP (C) and 7SU (D).

Neither combined protea nor combined erica nectar volume was related to patch size (Figures 4.7 A.1 and B.1; Table 4.2). Combined protea density was positively related with patch size, but combined erica biomass was independent of patch size (Figures 4.7 A.2 and B.2; Table 4.2). Total protea nectar availability (protea nectar volumes multiplied by combined protea density) also was positively related with patch size. Erica nectar availability (erica nectar volumes multiplied with combined erica biomass) was not significantly related with patch size but tended to decrease with patch size (Figures 4.7 A.3 and B.3; Table 4.2). There appeared to be a trade-off between proteas and ericas at different patch sizes, with proteas dominating in large patches and potentially outcompeting ericas. Ericas, on the other hand, occurred at higher biomass in small and medium patches.

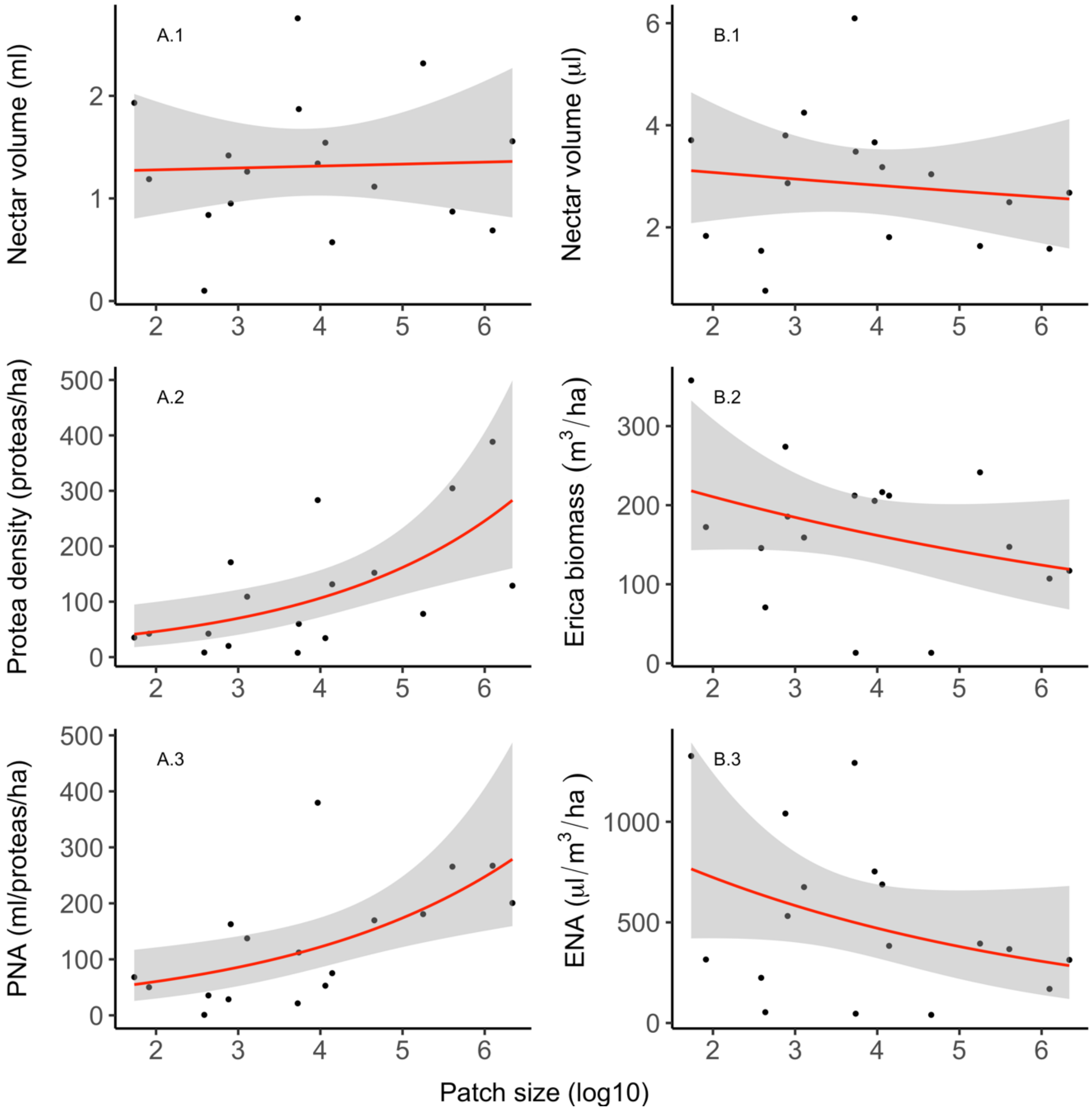


Figure 4.7: The relationships between combined protea nectar volume (A.1), combined protea density (proteas/ha) (A.2), and protea nectar availability (PNA - the two factors combined) (A.3) with patch size as well as between combined erica nectar volume (B.1), combined erica biomass (percentage/ha) (B.2), and erica nectar availability (ENA - the two factors combined) (B.3) with patch size. The grey shading represents the 95% confidence interval.

Table 4.2: Generalised linear model results for combined protea nectar, combined protea density and protea nectar availability (PNA - the two factors combined) with patch size as well as combined erica nectar, combined erica biomass and erica nectar availability (ENA - the two factors combined) with patch size.

Species	Value	Term	Estimate	Std. Error	t value	Pr(>|t|)
Protea	Nectar	Intercept	0.22	0.38	0.57	0.58
		Patch size (log10)	0.01	0.09	0.15	0.88
	Density	Intercept	2.99	0.64	4.67	**<0.001**
		Patch size (log10)	0.42	0.13	3.15	**0.007**
	PNA	Intercept	3.39	0.59	5.77	**<0.001**
		Patch size (log10)	0.35	0.12	2.83	**0.013**
Erica	Nectar	Intercept	1.21	0.34	3.59	**0.003**
		Patch size (log10)	-0.04	0.08	-0.51	0.62
	Biomass	Intercept	3.66	0.36	10.11	**<0.001**
		Patch size (log10)	-0.13	0.09	-1.4	0.18
	ENA	Intercept	5.06	0.53	9.62	**<0.001**
		Patch size (log10)	-0.21	0.14	-1.51	0.15

Bird abundance in relation to nectar volume

Although there was no significant relationship between Cape Sugarbird abundance and the combined protea flower nectar volumes (Table 4.3; Appendix 4.6), numbers of sugarbirds were positively correlated with protea nectar availability (Table 4.3; Figure 4.8 A.1). Similarly, there was no relationship between Southern Double-collared Sunbird abundance and combined erica nectar volumes per flower (Table 4.3; Appendix 4.6), but Southern Double-collared abundance was positively related to erica nectar availability (Table 4.3; Figure 4.8 C.1). Orange-breasted Sunbird abundance was not related to either combined erica nectar volumes per flower (Table 4.3; Appendix 4.5) nor erica nectar availability (Table 4.3; Figure 4.8 B.1). Both Cape Sugarbird abundance (Figure 4.8 A.2) and Orange-breasted Sunbird abundance (Figure 4.8 B.2) showed a positive relationship with patch size, while Southern Double-collared Sunbird abundance (Figure 4.8 C.2) had a negative relationship (see Chapter 3.4.7).

Table 4.3: Generalised linear model results for the relationships between selected bird species abundance and the relevant combined plant species nectar and the protea/erica nectar availability (combined protea/erica nectar multiplied with protea density/erica biomass).

Species	Term	Estimate	Std. Error	t value	Pr(> |t|)
Cape Sugarbird	Intercept	1.2	0.39	3.07	**0.008**
	Protea nectar	-0.16	0.28	-0.57	0.58
	Intercept	0.51	0.3	1.73	0.11
	PNA	0.0032	0.0015	2.2	**0.044**
Orange-breasted Sunbird	Intercept	0.07	0.4	0.17	0.87
	Erica nectar	0.15	0.12	1.25	0.23
	Intercept	0.32	0.27	1.2	0.25
	ENA	0.0024	0.0027	0.91	0.38
Southern Double-collared Sunbird	Intercept	0.62	0.22	2.87	**0.012**
	Erica nectar	0.09	0.07	1.31	0.21
	Intercept	0.56	0.12	4.74	**<0.001**
	ENA	0.0041	0.0011	3.59	**0.003**

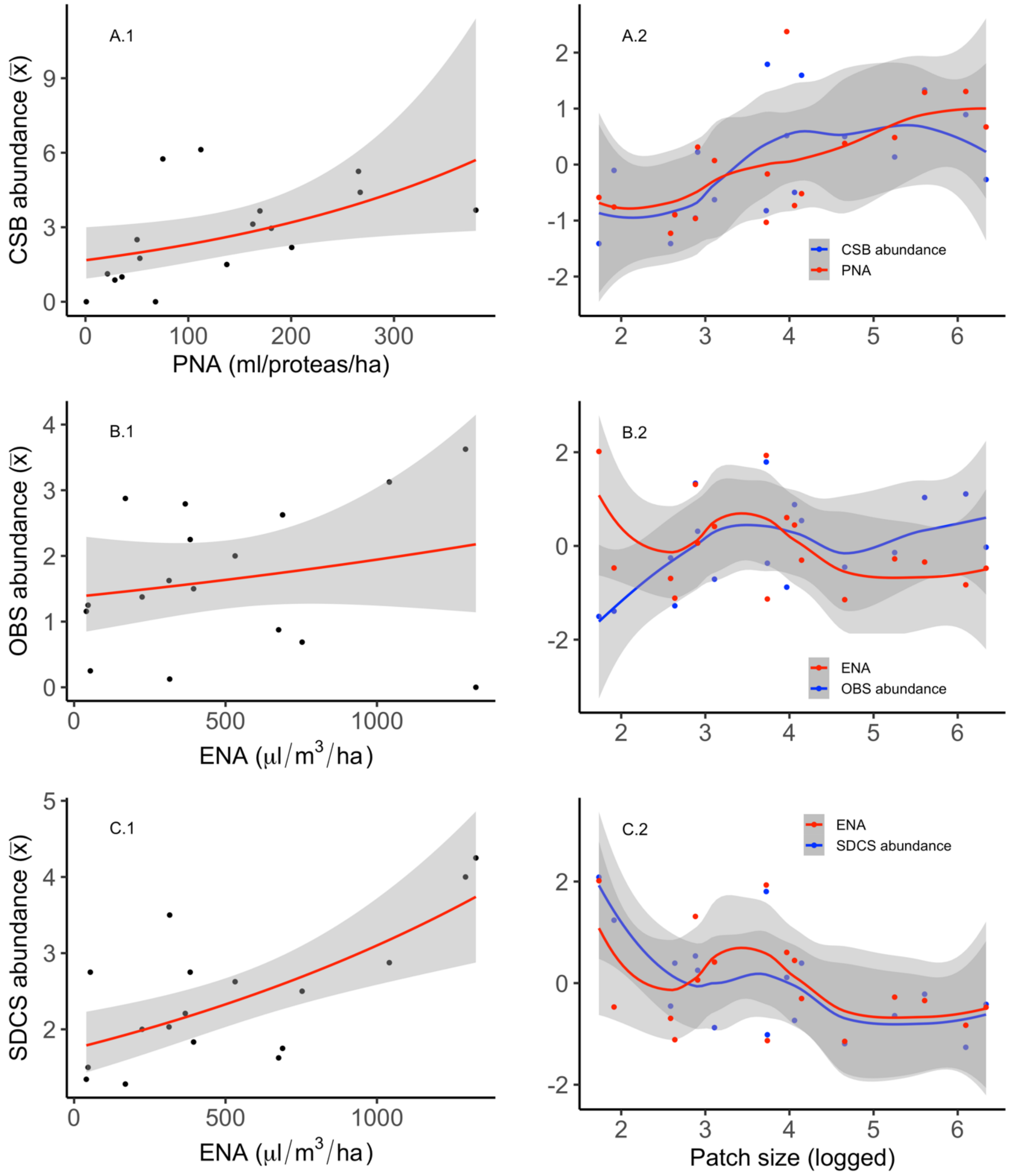


Figure 4.8: The relationships between Cape Sugarbird (CSB) abundance (A.1) and protea nectar availability (PNA - combined protea nectar volume multiplied with protea density), and Orange-breasted Sunbird (OBS) (B.1) and Southern Double-collared Sunbird (SDCS) (C.1) with erica nectar availability (ENA - combined erica nectar multiplied with erica biomass). I also show the scaled relationships with patch size of Cape Sugarbird (A.2) and PNA, and Orange-breasted Sunbird (B.2) and Southern Double-collared Sunbird (C.2) with ENA. The grey shading represents the 95% confidence interval.

Nectar of bagged flowers compared with unbagged flowers

The mean nectar volume in bagged flowers was greater than in unbagged flowers for all three species (Figure 4.9, Appendices 4.7 and 4.8), although the difference was not significant for *P. mundii* likely because of the small sample size (Appendices 4.7 and 4.8). There was no significant difference in mean nectar concentration between bagged and unbagged flowers for

P. mundii but surprisingly, nectar concentrations were greater in bagged flowers of both *P. neriifolia,* and *E. discolor* (Figure 4.9; Appendices 4.7 and 4.8). The lower nectar concentration percentage from unbagged flowers presumably results from the relatively greater amount of remnant water diluting nectar samples (Aizen 2003; Bartoš et al. 2012).

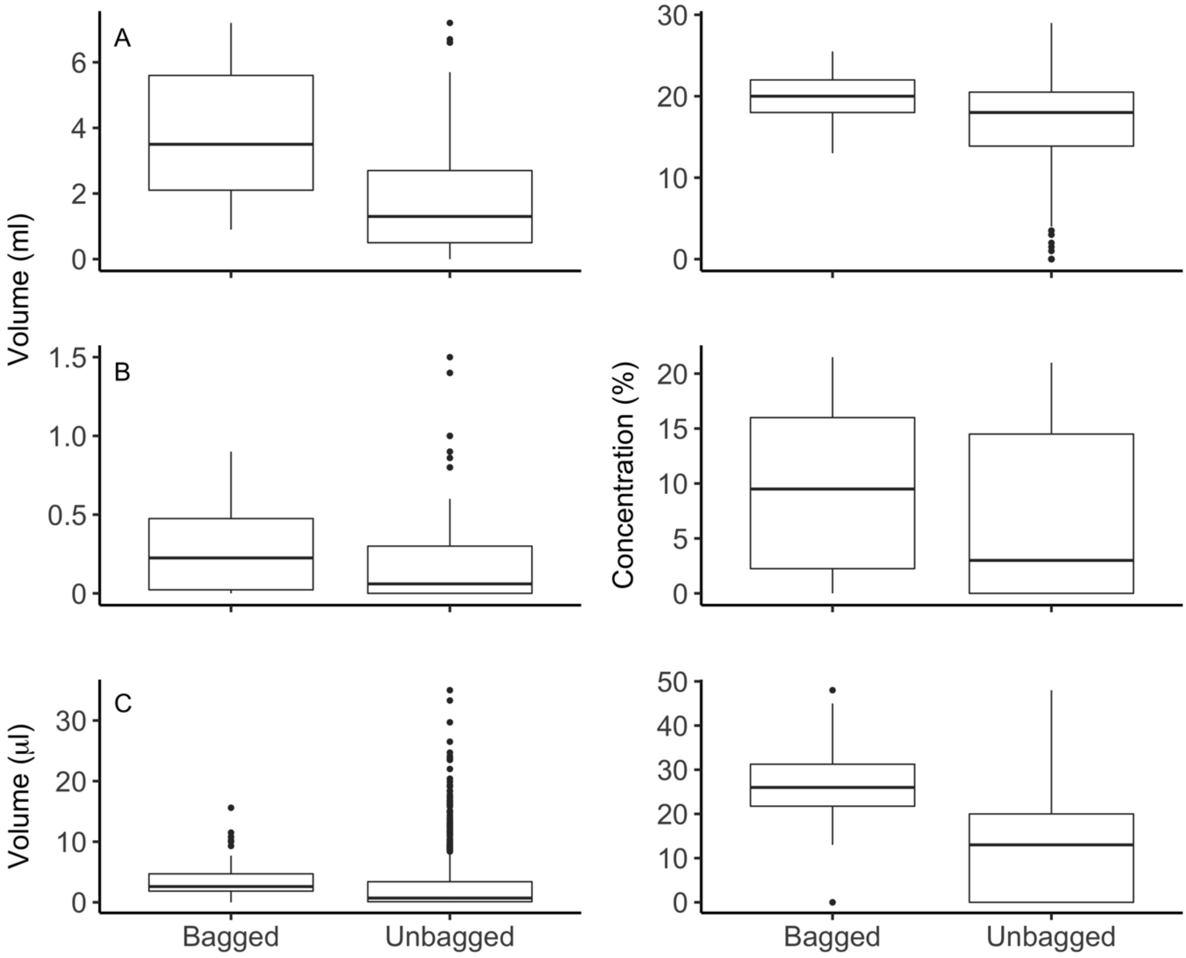


Figure 4.9: Boxplots for nectar volume and concentration comparing bagged and unbagged flowers of *P. neriifolia* (A), *P. mundii* (B) and *E. discolor* (C).

Discussion

My findings showed that habitat fragmentation affected nectar availability of the more common protea and erica species, as well as the respective bird species that feed on them. This follows the finding that the sunbirds and Cape Sugarbirds will respectively utilise erica and protea nectar if they have access (see Chapter 3). Overall, it seems that there were as expected a strong positive relationship between the number of protea flowers per month, the amount of nectar available and then correspondingly the number of Cape Sugarbirds per month over the study area (Table 4.1; Figures 4.2 and 4.3). Proteas mainly flowered seasonally, with the time of peak flowering varying in relation to rainfall (Carlson et al. 2011). In the eastern CFR, where rain falls all-year, the peak flowering period is in January – March (Figure 4.2; Heelemann et al. 2008; Kraaij et al. 2013b). The peak flowering period seems to be similar for the study area, but it was unfortunately unclear because of the study period ending before flowering peaked (Figure 4.2). This peak period contrasts with the western region of the CFR, where the protea flowering peaks in May – July overlaps with winter rainfall (Heelemann et al. 2008; Carlson et al. 2011). Cape Sugarbird are tightly associated with proteas for food (nectar and insects) and breeding (Daniels et al. 2001; Potgieter et al. 2008). Their breeding coincides with protea flowering (Calf et al. 2003b; Schmid et al. 2016). Cape Sugarbirds, like many other bird species, move between areas and abandon their breeding areas seasonally (Broekhuysen 1959; Altwegg & Underhill 2006; Mulwa et al. 2013; Geerts et al. 2020). The seasonal patterns shown here in flowering and nectar availability suggests that Cape Sugarbirds move to track food resources (Calf et al. 2003a).

Other studies have suggested, although there is only limited evidence, that aspects such as flowering periods, nectar and pollen resource availability and thus pollinator behaviour can be impacted by habitat fragmentation (Xiao et al. 2016). In the case of this study, the geographic area was too small and the number of sites too few to investigate the impact of habitat fragmentation on flowering phenology.

Contrary to my predictions, there was no difference in nectar volume per flower between small and medium patches, especially for the widespread and abundantly occurring *P. neriifolia* and *E. discolor* (Figure 4.4). Between patch variability was high when I considered the combined per flower nectar volume relationship with patch size for ericas, and then especially for proteas (Figures 4.7 A.1 and B.1). Nectar volume variability appeared to be greater in small and medium patches, with less variability and a more defined pattern shown in large patches, especially for ericas (Table Figures 4.7 A.1 and B.1). For the small patches I could show neither of the fragmentation effects predicted regarding nectar availability per flower. This finding was likely a true reflection of the situation as there is often high natural variability in nectar availability in flowers as well as in nectar sources and availability between different areas and their surrounding matrices (Wolff 2006). A study in Pernambuco, northeast Brazil, revealed significant differences between fragments of Atlantic rainforest when comparing nectar volumes and sugar composition ratios of selected understory tree species (Braun 2010). They found high variability in rainforest fragments of both nectar volumes and sugar composition ratios (Braun 2010). The researchers also ascribed the high variability in nectar volume between forest fragments to natural variation (Braun 2010). They did though suggest that the differences found in sugar composition ratios between rainforest fragments were likely a negative effect of habitat fragmentation (Braun 2010). I did not compare nectar sugar composition and composition ratios between habitat fragments, but it might be worth considering for future studies. I also cannot discount the possibility that the lack of a defined pattern is the result of an inadequate sample size to reveal differences between patches. It is also worth considering that the similar nectar volume per flower between the small and medium patches effectively show that bird flower utilisation between the two size categories is the same. For Cape Sugarbird this can be explained by their apparent easy of mobility between patches while for the sunbirds, Orange-breasted Sunbird is replaced by Southern Double-collared Sunbird in the small patches.

The reduced amounts of nectar per flower among *P. neriifolia* and *E. discolor* in large compared with medium patches suggest that sunbirds and sugarbirds took more nectar per flower in large patches (Figures 4.4, 4.5 and 4.6). This increased utilisation is supported by the higher abundance per point-count found of both Cape Sugarbird and Orange-breasted Sunbird in larger patches (Figures 3.7 and 3.8). This pattern of higher nectar utilisation with higher bird abundance was also found in a study in proteoid fynbos in the Western Cape of South Africa where per plant visitation rate, as a proxy for flower nectar utilisation, was positively related to nectarivore population size (more so for Cape Sugarbird than for Orange-breasted Sunbird) (Schmid et al. 2016).

Although individual flowers had less nectar in large patches, a result of being fed on more, if protea nectar availability (protea nectar combined with protea plant density) is considered, large patches had overall more nectar than medium patches (Figure 4.7 A.3; Table 4.2). The higher protea density in large patches is likely a reflection of less external disturbances and influences over time and better implemented long-term management actions, for example appropriate fire interval periods, resulting in increased ecological integrity (Lienert & Fischer 2003; Kraaij et al. 2013a). A higher abundance of Cape Sugarbirds with increased nectar availability per patch supports the findings in Chapter 3 that Cape Sugarbird abundance increased with patch size (Table 4.3; Figures 3.7 and 4.8 A). I detected Cape Sugarbirds in all study patches (at least occasionally), which is to be expected as they are a mobile species that undertakes seasonal movements to track resources (Broekhuysen 1959). An important conservation question to ask is: at what stage will a fynbos area not be able to supply sufficient resources to attract and then sustain Cape Sugarbirds? Schmid et al. (2016) estimated that Cape Sugarbirds are unlikely to persist in a fynbos area if there is less than 3000 g sugar/ha. Numbers of Cape Sugarbirds increase faster than those of Orange-breasted Sunbirds as nectar availability increases, with the presence of Cape Sugarbird territories strongly correlated with sugar density (Calf et al. 2003a; Schmid et al. 2016). There is thus a strong likelihood that Cape Sugarbirds will not establish breeding territories in smaller-sized patches because of a lack of sufficient available nectar. However, I did not record breeding activity, so cannot confirm this for the study. Small patches, while providing some seasonal food sources, may thus be less viable ecologically for Cape Sugarbirds than large patches and may need to be part of a larger network of intact habitat patches. In the following chapter I investigate whether protea and erica seed production differs among study patches. Specifically, I test whether fewer viable seeds develop in small patches where there are fewer Cape Sugarbirds.

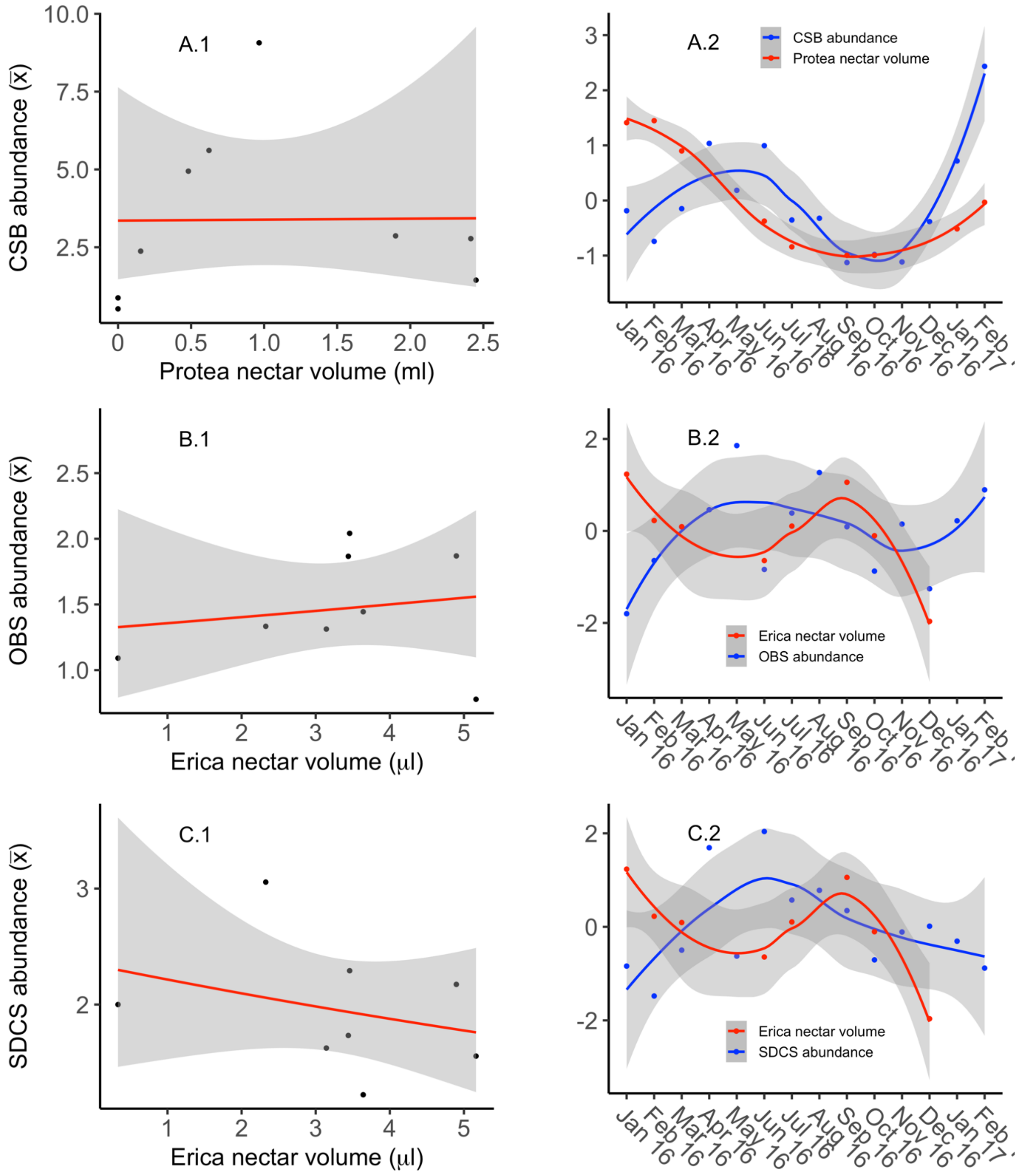
Orange-breasted Sunbird did not show a strong relationship with the amount of erica nectar available per patch, whilst Southern Double-collared Sunbird increased in abundance as erica nectar availability increased (Table 4.3; Figure 4.8). Southern Double-collared Sunbirds are generalists that make use of a variety of nectar sources and habitats surrounding a patch, while the fynbos specialist Orange-breasted Sunbird is more specifically associated with ericas and other fynbos plants (e.g. proteas and bulbs) in intact fynbos habitat (Brown 2005b; Smith & Tree 2005; Geerts et al. 2020). As shown in Chapter 3 and suggested here with the lower erica nectar availability as patch size increases, Southern Double-collared Sunbird abundance had a negative relationship with increasing patch size (Table 4.3; Figures 3.8 and 4.8). The increase in Southern Double-collared Sunbird abundance was thus likely confounded by the fact that the small patches, where erica nectar availability was higher, was also where the sunbirds abundance was likely to be higher because of the suitability of the surrounding matrix habitat for them.

Conclusions

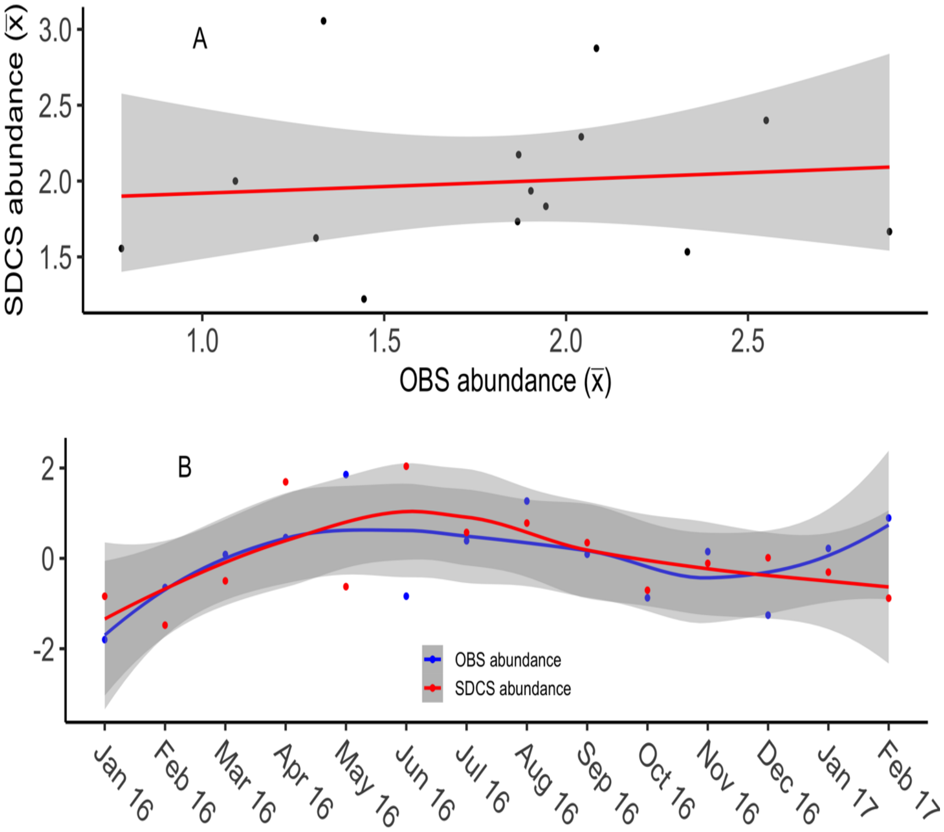
I expected that flower nectar availability between patches would show a more definitive fragmentation effect, but inter-patch variation was too great to show clear patterns, especially among the small and medium patches. However, I still gained some valuable insights: the relationships shown here between sugarbirds and sunbirds with protea and erica nectar respectively confirm that overall nectar availability, rather than individual flower nectar availability, determine bird abundance (Coetzee et al. 2021). The mechanism responsible for the negative effect of fragmentation on nectar availability was tied to the number of plants per patch, which increased with patch size for proteas and decreases for ericas. It is thus important to promote that intact fynbos habitats, regardless of patch size, should be maintained and increased in number and size. That will allow for an increase in the amount of available nectar-producing plants, to draw and maintain a variety of fynbos nectarivore bird species.

Appendices

Appendix 4.1: The mechanism used to extract nectar from protea flowers, comprising half a two-litre bottle as a funnel with a test tube at the end, and a plastic bag, tied with a ca 1.5 m length rope around the stem of a protea flower, once it is placed into the funnel, to hold it all together. Rotating the device at ca 1.5 revolutions per second (for a minute) generates centrifugal force to extract the nectar.



Appendix 4.2: The relationships between Cape Sugarbird abundance per month (A.1) and protea nectar volume per month and Orange-breasted Sunbird (B.1) and Southern Double-collared Sunbird (C.1) per month and erica nectar volume per month. I also show how the scaled abundance of each of the respective variable pairs relate and compare with each other per month (A.2, B.2 and C.2). The grey shading represents the 95% confidence interval.



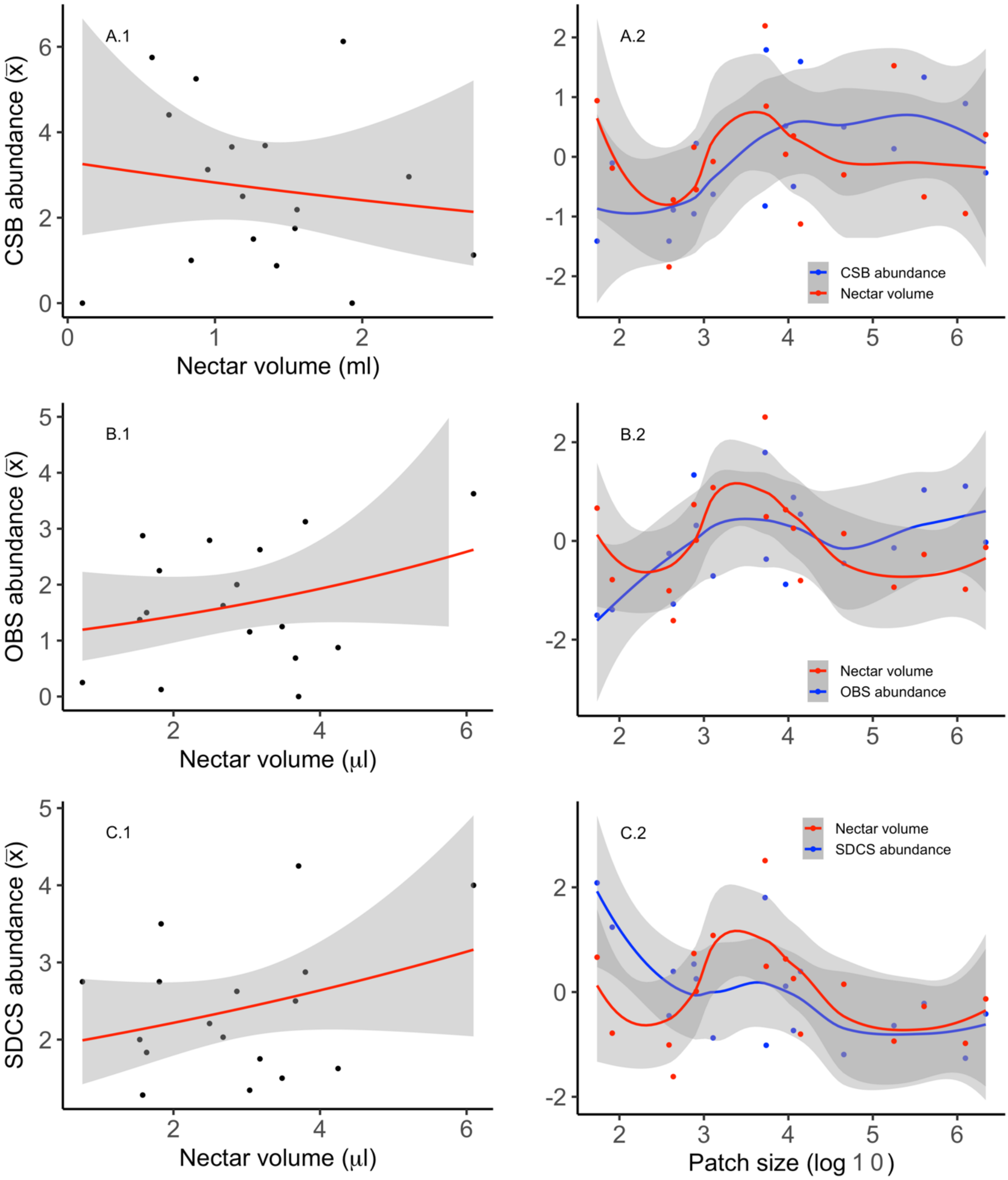
Appendix 4.3: The relationship between average Orange-breasted Sunbird per month and average Southern Double-collared Sunbird per month for all the patches. I also see how the scaled abundance of both species vary per month and relative to each other. The grey shading represents the 95% confidence interval.

Appendix 4.4 Sample size, mean (with standard deviation) and median (with interquartile range) for nectar volume for small-, medium- and large-sized patch categories. The statistics for nectar volume for each of the selected plant species are for all the field survey periods they were collected and then also for *E. discolor* and *P. neriifolia* per field survey period that they were collected. Volume for the proteas is in ml and for the ericas in µl.

Year/ Species	**Species/ Survey Period**	**Size category**	**N**	**Mean**	**SD**	**Median**	**IQR**
All survey periods	*Protea neriifolia*	Small	89	1.48	1.5	0.9	2.1 (0.3 - 2.4)
		Medium	161	1.67	1.52	1.3	2.2 (0.5 - 2.7)
		Large	80	1.38	1.56	0.8	2.17 (0.05 - 2.3)
	Protea mundii	Small	25	0.38	0.41	0.3	0.6 (0 - 0.6)
		Medium	34	0.18	0.29	0.04	0.28 (0 - 0.28)
		Large	40	0.15	0.28	0.05	0.09 (0.01 - 0.1)
	Erica discolor	Small	560	2.68	4.19	0.7	3.53 (0.1 - 3.63)
		Medium	560	3.27	4.95	0.9	4.3 (0.2 - 4.5)
		Large	240	2.25	3.53	0.7	2.9 (0.1 - 3)
	Erica densifolia	Small	92	3.71	5.02	1.3	5.25 (0.2 - 5.45)
		Medium	95	3.67	5.5	0.8	5.55 (0.1 - 5.65)
		Large	100	3.19	3.8	1.2	4.43 (0.3 - 4.73)
Erica discolor	1SU	Small	140	3.88	5.19	2	4.6 (0.28 - 4.88)
		Medium	140	4.35	5.62	2.2	5.75 (0.58 - 6.33)
		Large	60	4.14	4.53	3	5.23 (0.45 - 5.68)
	3WI	Small	140	2.42	3.88	0.65	2.9 (0.1 - 3)
		Medium	140	3.1	4.74	0.95	4.5 (0.1 - 4.6)
		Large	60	2.2	3.29	0.45	2.98 (0.1 - 3.08)
	5SP	Small	140	4.14	4.36	2.35	5.13 (0.98 - 6.1)
		Medium	140	5.24	5.5	3.3	7.03 (1 - 8.03)
		Large	60	2.38	3.4	1.5	2.3 (0.58 - 2.88)
	7SU	Small	140	0.28	0.41	0.2	0.2 (0.1 - 0.3)
		Medium	140	0.41	1.01	0.2	0.2 (0.1 - 0.3)
		Large	60	0.29	0.28	0.2	0.3 (0.1 - 0.4)
Protea neriifolia	1SU	Small	44	2.43	1.55	2.4	2.38 (0.98 - 3.35)
		Medium	77	2.57	1.54	2.6	2.3 (1.3 - 3.6)
		Large	30	2.24	1.54	2.05	1.77 (1.23 - 3)
	3WI	Small	22	0.65	0.7	0.45	0.9 (0.1 - 1)
		Medium	38	0.84	0.82	0.65	1.12 (0.13 - 1.25)
		Large	20	0.13	0.31	0	0.04 (0 - 0.04)
	8SU	Small	23	0.45	0.5	0.4	0.6 (0.06 - 0.65)
		Medium	46	0.85	1	0.45	1.28 (0.04 - 1.33)
		Large	30	1.34	1.55	0.75	2.02 (0.1 - 2.13)

Appendix 4.5 Pairwise comparison from linear model results for the relationships between patch size categories for nectar volume. The statistics for nectar volume for each of the selected plant species are for all the field survey periods they were collected in and then also for *E. discolor* and *P. neriifolia* per field survey period that they were collected in.

Year/ Species	**Species/ Survey period**	**Size category**	**Estimate**	**St. Error**	**df**	**t value**	**Pr(>|t|)**
All	*Protea neriifolia*	Small - Medium	-0.08	0.08	327	-1.11	0.51
		Small - Large	0.07	0.09	327	0.79	0.71
		Medium - Large	0.15	0.08	327	1.95	0.13
	Protea mundii	Small - Medium	0.14	0.06	96	2.43	**0.04**
		Small - Large	0.16	0.06	96	2.94	**0.01**
		Medium - Large	0.02	0.05	96	0.47	0.89
	Erica discolor	Small - Medium	-0.11	0.05	1357	-2.05	**0.1**
		Small - Large	0.07	0.07	1357	1.09	0.52
		Medium - Large	0.18	0.07	1357	2.68	**0.02**
	Erica densifolia	Small - Medium	0.06	0.14	284	0.47	0.89
		Small - Large	0.01	0.14	284	0.07	1
		Medium - Large	-0.06	0.13	284	-0.41	0.91
Erica discolor	1SU	Small - Medium	-0.08	0.11	337	-0.77	0.72
		Small - Large	-0.1	0.14	337	-0.71	0.76
		Medium - Large	-0.02	0.14	337	-0.12	0.99
	3WI	Small - Medium	-0.14	0.1	337	-1.38	0.35
		Small - Large	0.05	0.13	337	0.4	0.92
		Medium - Large	0.19	0.13	337	1.47	0.31
	5SP	Small - Medium	-0.15	0.1	337	-1.62	0.24
		Small - Large	0.36	0.12	337	2.89	**0.01**
		Medium - Large	0.51	0.12	337	4.14	**<0.001**
	7SU	Small - Medium	-0.04	0.03	337	-1.46	0.31
		Small - Large	-0.02	0.04	337	-0.41	0.91
		Medium - Large	0.03	0.04	337	0.72	0.75
Protea neriifolia	1SU	Small - Medium	-0.05	0.09	148	-0.56	0.84
		Small - Large	0.06	0.11	148	0.51	0.87
		Medium - Large	0.11	0.1	148	1.05	0.55
	3WI	Small - Medium	-0.1	0.1	77	-1.07	0.53
		Small - Large	0.32	0.11	77	2.88	**0.01**
		Medium - Large	0.43	0.1	77	4.26	**<0.001**
	8SU	Small - Medium	-0.17	0.12	96	-1.41	0.34
		Small - Large	-0.34	0.13	96	-2.58	**0.03**
		Medium - Large	-0.17	0.11	96	-1.51	0.29



Appendix 4.6: The relationships between Cape Sugarbird (CSB) (A.1) and combined protea nectar volume, and Orange-breasted Sunbird (OBS) (B.1) and Southern Double-collared Sunbird (SDCS) (C.1) with combined erica nectar volume. The scaled relationships of Cape Sugarbird (A.2) and combined protea nectar, and Orange-breasted Sunbird (B.2) and Southern Double-collared Sunbird (C.2) with combined erica nectar are also shown. The grey shading represents the 95% confidence interval.

Appendix 4.7: Linear model results for the nectar volume and concentration relationships between bagged and unbagged flowers of selected protea and erica species.

Species	**Volume/Concentration**	**Term**	**Estimate**	**Std. Error**	**t value**	**Pr(> |t|)**
Protea neriifolia	Volume	Intercept	1.47	0.13	11.02	**<0.001**
		Unbagged	-0.61	0.14	-4.39	**<0.001**
	Concentration	Intercept	19.38	1.64	11.84	**<0.001**
		Unbagged	-3.44	1.69	-2.03	**0.043**
Protea mundii	Volume	Intercept	0.22	0.05	4.22	**<0.001**
		Unbagged	-0.06	0.06	-0.98	0.33
	Concentration	Intercept	9.56	1.78	5.36	**<0.001**
		Unbagged	-2.75	1.94	-1.42	0.16
Erica discolor	Volume	Intercept	1.38	0.11	12.14	**<0.001**
		Unbagged	-0.51	0.12	-4.42	**<0.001**
	Concentration	Intercept	26.65	1.51	17.69	**<0.001**
		Unbagged	-15.38	1.54	-9.99	**<0.001**

Appendix 4.8 Sample size, mean (with standard deviation) and median (with interquartile range) for nectar volume and concentration for both bagged and unbagged flowers for each of the selected plant species. * - volume for *P. neriifolia* and *P. mundii* is in ml and for *E. discolor* it is in µl.

Species	**Bagged/ Unbagged**	**N**	**Volume (ml/µl)***				**Concentration (%)**			
			Mean	**SD**	**Median**	**IQR**	**Mean**	**SD**	**Median**	**IQR**
Protea neriifolia	Bagged	17	3.84	2.15	3.5	3.5 (2.1 - 5.6)	19.38	3.56	20	4 (18 - 22)
	Unbagged	248	1.76	1.54	1.3	2.2 (0.5 - 2.7)	15.95	6.9	18	6.62 (13.88 - 20.5)
Protea mundii	Bagged	18	0.28	0.28	0.22	0.46 (0.02 - 0.48)	9.56	8.07	9.5	13.75 (2.25 - 16)
	Unbagged	97	0.22	0.33	0.06	0.3 (0 - 0.3)	6.8	7.46	3	14.5 (0 - 14.5)
Erica discolor	Bagged	55	3.79	3.21	2.6	2.85 (1.85 - 4.7)	26.65	9.46	26	9.5 (21.75 - 31.25)
	Unbagged	1243	2.65	4.26	0.7	3.3 (0.1 - 3.4)	11.28	11.24	13	20 (0 - 20)

Chapter 5: The impact of habitat fragmentation on erica and protea seed-set in the Cape Floristic Region

Abstract

Plants that only set seed when they are fertilised may be reliant on specific pollinators. In a fragmented landscape, the lack of adequate habitat and food and other resources can result in a paucity of pollinators. Over time, the consequence can be the loss of pollinator-reliant plant species. In the fynbos vegetation of the Cape Floristic Region (CFR) of South Africa, bird-pollinated plants are pollinated by a small number of nectarivore bird species: Cape Sugarbirds (*Promerops cafer*) are the key avian pollinators for proteas and Orange-breasted Sunbirds (*Anthobaphes violacea*) for ericas. In a study area in fragmented fynbos habitat in the western Tsitsikamma in the eastern region of the CFR, I investigated if habitat fragmentation influenced seed-set for *Erica discolor* and *Protea neriifolia* flowers. Contrary to expectations, *E. discolor* seed-set was lower in large patches, indicating a fragmentation benefit where additional pollinators were likely introduced from the surrounding non-habitat matrix to small patches. This held true for each of the three survey periods investigated. I did not find a fragmentation effect on *P. neriifolia* seed-set, which reflects that Cape Sugarbirds managed to frequent all patches in the study. *Erica discolor* had higher seed-set in small patches, which might be explained by high sunbird density, thanks mainly to large numbers of Southern Double-collared Sunbirds visiting from the surrounding non-fynbos matrix. However, *E. discolor* seed-set was not significantly related to Southern Double-collared Sunbird abundance, but Orange-breasted Sunbird abundance showed a significant negative relationship. Orange-breasted Sunbird abundance was negatively affected by fragmentation. Their relationship with *E. discolor* seed-set was thus more a reflection of the higher effective pollination rates in the smaller patches, than their ability to pollinate the plants in the large patches. *Protea neriifolia* seed-set showed no relationship with Cape Sugarbird abundance, which increased with patch size. There was no relationship between either *E. discolor* or *P. neriifolia* seed-set and the associated nectar volume in each patch. The results show that habitat fragmentation had overall limited impact on seed-set in the study area. Depending on the species investigated, there might even be a net increase in seed-set.

Introduction

Plant pollination can fail at several stages, including pre-dispersal failure (e.g. sterile pollen, or destruction or loss of pollen), dispersal failure (e.g. lack of pollinators), and post-dispersal failure (e.g. insufficient, old or poor quality pollen; Wilcock & Neiland 2002; Latty & Dakos 2019). Low pollinator abundance can exacerbate each of these stages (Aguilar et al. 2019). How vulnerable a plant species' reproduction is to low pollinator abundance is determined by its dependence on pollinators for seed-set, how specific the pollinators involved are, and its dependence on seeds for reproduction (Bond 1994; Teixido et al. 2022). Many plant species co-evolved with and rely on their pollinators for pollination (Johnson & Anderson 2010; Angoh et al. 2017). Some plants rely on generalist pollinators that can pollinate a variety of plant species, while others rely on specialist pollinators (Johnson & Nicolson 2008; Brown et al. 2011; Armbruster 2017). Some well-known examples of specialist insect pollination systems from around the world include *Yucca spp*. and Yucca moths (family Prodoxidae), *Ficus spp.* and Fig wasps (family Agaonidae), Senita cactus (*Lophocereus schottii*) and Senita moths (*Upiga virescen*s) and Leafflowers (*Glochidion spp.*) and Leafflower moths (*Epicephala spp*; Pellmyr et al. 2020).

Plants that are dependent on pollinators for pollination may be at risk from catastrophic environmental disturbance or through habitat fragmentation and landscape alteration (Wilcock & Neiland 2002; Teixido et al. 2022). After two intense hurricane seasons from 1995 - 1997, the fruit set of the Bahama Swamp-bush (*Pavonia bahamensis*) was severely reduced on San Salvador Island, Bahamas (Rathcke 2000). This was attributed to pollination limitation caused by declines in two bird pollinators, Bananaquits (*Coereba flaveola*) and Bahama Woodstars (*Calliphlox evelynae*) (Rathcke 2000). Habitat fragmentation and landscape alteration also can result in pollen and pollination limitation in small and isolated habitat fragments (Aguilar et al. 2006; Teixido et al. 2022). These limitations can be because of lower pollinator species richness an abundance, or changes in foraging behaviour patterns that result in fewer visits per flower and/or smaller average pollen loads per visit (Jennersten 1988; Lamont et al. 1993; Aizen & Feinsinger 1994; Didham et al. 1996; Cunningham 2000). The shortage of pollinators in fragmented and altered habitats, can be because of a lack of available food resources, nesting sites and larval host plants, and by changing the presence and/or abundance and the behaviour of their predators and parasites (Donaldson et al. 2002; Aguilar et al. 2006, 2019; Aslan et al. 2013). How a specific pollinator will be affected depends on the species' characteristics (e.g. dispersal ability), feeding range and the variety of food sources on which they feed (Montero-Castaño & Vilà 2012). Vertebrate pollinators such as bats and birds, through their ability to traverse longer distances, are generally less affected in their role as pollinators in fragmented environments than insects (Aguilar et al. 2019).

The loss of a pollinator can lead to the decline and eventually the extinction of the reliant plant species (Geerts & Pauw 2012; Latty & Dakos 2019; Teixido et al. 2022). The critically endangered *Brighamia insignis*, a lobeliad endemic to the islands of Kaua'i and Ni'ihau, Hawai'i, lost its moth pollinator because of human induced habitat loss, overexploitation and invasive species, and is not able to reproduce (less than 1% of flowers form fruit; Walsh et al. 2019). Without intensive human-assisted cross-pollination, the species is likely to go extinct (Walsh et al. 2019). On the islands of Craigieburn and Ohau, New Zealand, endemic mistletoes, *Peraxilla colensoi* and *P. tetrapetala*, have shown considerable decline since 1840 because of pollen limitation because of a lack of insufficient bird pollinators, Bellbirds (*Anthornis melanura*) and Tuis (*Prosthemadera novaeseelandiae*) (Robertson et al. 1999). Without efforts to conserve these bird species, the endemic mistletoes and many other New Zealand plants, are predicted to decline further (Robertson et al. 1999).

There are only a small number of specialist nectarivore bird pollinators in the CFR fynbos (Rebelo 1987; Whelan et al. 2008; Geerts et al. 2020). The fynbos-endemic Cape Sugarbirds (*Promerops cafer*) and Orange-breasted Sunbirds are the key avian pollinators for proteas and ericas, respectively (Geerts & Pauw 2012; Pauw & Johnson 2018). In a fragmented landscape in the eastern, all-year rainfall region of the Cape Floristic Region (CFR), I investigate if fragmentation influences the pollination role of these and generalist nectar feeding bird species in *Protea neriifolia,* and *Erica discolor* flowers. I consider if these plant species' seed-set is related to their respective sunbird and sugarbird abundance in each patch. I further also test whether nectar availability is related to seed-set in each patch.

Methods

Study area, patches, survey blocks, point-counts and other variables

The study area in the western Tsitsikamma in the CFR comprises 17 fynbos patches of varied sizes (Chapter 2). I undertook the fieldwork in eight approximately six-week survey periods during 2016 - 2017 (Table 3.1). During each survey period, I undertook 10-minute bird point-counts from set locations in each patch (Chapter 3). There were one to four locations per patch, depending on the patch size. I also recorded several vegetation variables during each survey period and point-count including relative density of proteas and ericas and vegetation biomass around each point-count (Chapters 2 and 3). I also conducted arial drone surveys to estimate protea densities for each site (Chapter 2). During every second survey period I collected protea and erica flowers and measured extracted nectar volumes and concentration (Chapter 4).

Seed collection and counting

During the second survey period I randomly selected 10 *P. neriifolia* flowerheads (estimated to have flowered earlier in the season) in each patch. I stored flowerheads in a sealed container for two months to dry until the seeds were loose. Care was taken to ensure that the seeds of each flowerhead were collected and kept separate. I hand-counted the seeds and identified pollinated (viable) seeds (can potentially germinate) as plump and well-rounded (Steenhuisen & Johnson 2012). I also recorded for each flowerhead the proportion of the base where seeds were destroyed by, for example, beetles or insect larvae (Nottebrock et al. 2017b). Accounting for how much of the base was destroyed, I estimated what the pollinated (viable) and unpollinated (non-viable) seed counts would have been if the base was whole. This estimated value was used in analyses.

To assess seed-set in *E. discolor* I marked 20 flowers during the first survey period. In the second survey period, approximately 8-weeks later, I collected the ripe fruits (Angoh et al. 2017). I repeated the flower marking in the third, fifth and seventh survey periods whilst ripe fruit collection were repeated for the fourth, sixth and eight survey blocks. On collection, I recorded the number of fruits (not lost to e.g., weather events or herbivory). I lost most fruits during the first survey block as I underestimated the rate that the fruits would ripen during the warm summer conditions: fruits had expelled their seeds by the time of collection. Subsequent collections were shortened to six weeks so that fruits were collected prior to dehiscence.

Each collected fruit was opened, and the seeds evenly spread with a dissecting needle on a 9 x 7 cm white paper (based on camera viewfinder dimensions) (Figure 5.1). I set a Canon PowerShot SX60 HS camera up on a tripod directly above so that the paper filled the frame (4608 x 3456 pixel canvas and 96 dpi resolution) (Figure 5.2). I set lights up for an even light spread and to minimise seed shadows (Figure 5.2). To prevent blurred photographs, I set the camera to a 2 second delay after pressing the button. Using ImageJ software, I automated the counting of the pollinated (viable) and non-pollinated (non-viable) seeds for each fruit (Rueden et al. 2017). ImageJ has been validated as an alternative to manual counting of erica seeds (Angoh et al. 2017, 2021). Pollinated seeds were visibly larger and plump compared with the smaller and shriveled non-pollinated seeds (Turner 2012). As there is some overlap in size between pollinated and un-pollinated seeds, I repeated and recorded the seed count three times for each fruit using different size threshold levels (600, 800 or a 1000 pixels). I used the following ImageJ steps and settings to count *E. discolor* seeds. Run the "colour thresholder" macro and then the "binary analyse" macro (set option - "black background" to false). Next run “make binary” and then “fill holes”. Finally, run “analyse particles” with “show outlines” selected and the “display results”, “clear results” and “summarise” options toggled to on. For "analyse particles", "size" was set to 15 - 600 (or 800 or a 1000 dependent on threshold) pixels for non-viable seeds, to 601(or 801 or 1001) - 1750 pixels for viable seeds and 1751 - 3000 pixels for double (overlapping) viable seeds. I estimated size ranges for the different categories by pixel area measurement of seeds visually assessed on the original photographs. I also visually determined for each double if it was one large seed or two or more overlapping seeds.

Figure 5.1: *Erica discolor* seeds spread out on a 9 x 7 cm white paper before taking a photograph.

Figure 5.2: A camera set-up above a white paper with *E. discolor* seeds to ensure that a useable and comparable photograph can be taken.

Data Analysis

I conducted analyses in R using the RStudio development framework (R Core Team 2020; RStudio Team 2020) and the "tidyverse" collection of packages (Wickham et al. 2019). I used generalised linear models, with a quasi-Poisson link function (to account for over-dispersion), to test if there were differences in viable *P. neriifolia* and *E. discolor* seeds between small, medium and large patches overall and for each survey period that data was collected for (see Table 3.1 for survey period acronyms used). I used the 800-pixel threshold for E. discolor as I visually assessed that it gave the best distribution between viable and unviable seeds compared with the two other thresholds. For all *P. neriifolia* analyses, I used the estimated viable seeds values after confirming that there was a non-significant difference in the percentage of protea bases destroyed between size categories. The convention used for boxplots are the minimum value, a box with the first quartile, median and third quartile, and the maximum value. For the unbagged flower nectar volume differences between patch size categories, I also show the raw point distribution and in red, pairwise comparison (with standard error) with same letters indicating no difference.

I used generalised linear models with a quasi-Poisson link function to predict seed-set for *P. neriifolia* and *E. discolor* based on patch size (log transformed). For *E. discolor* I used segmented (broken-line) analyses after I anticipated, based on visual inspection of the linear model figure, that the relationship may have a significant inflection (Muggeo 2003, 2008, 2016, 2017). I also used generalised linear models with a quasi-Poisson link function to investigate the relationships between *P. neriifolia* viable seeds and Cape Sugarbird abundance and *E. discolor* viable seeds and the abundance of Orange-breasted Sunbirds and Southern Double-collared Sunbirds. Lastly, generalised linear models with a quasi-Poisson link function were used to determine if there were relationships between *P. neriifolia* viable seeds and nectar volume and protea nectar availability (nectar volume multiplied with protea density) and *E. discolor* viable seeds and nectar volume and erica nectar availability (nectar volume multiplied with erica biomass).

Results

Comparing flower seed-set among patches

Erica discolor had significantly more viable seeds in small patches than in either medium or large patches (Figure 5.3; Appendix 5.1). This same pattern held for each of the survey periods included but only in 6SP did small patches have significantly more viable seeds than large patches (Figure 5.4; Appendix 5.1). *Protea neriifolia* showed no significant differences in viable seeds (estimated) between patch size categories (Figure 5.3; Appendix 5.1). *Erica discolor* viable seeds showed a significant negative relationship with patch size (Table 5.1). Segmented analysis for the same analysis showed a significant negative relationship for the first segment until the breakpoint and then no relationship for the second segment (Table 5.1; Figure 5.5 A). *Protea neriifolia* viable seeds showed no relationship with patch size (Table 5.1; Figure 5.5 B).

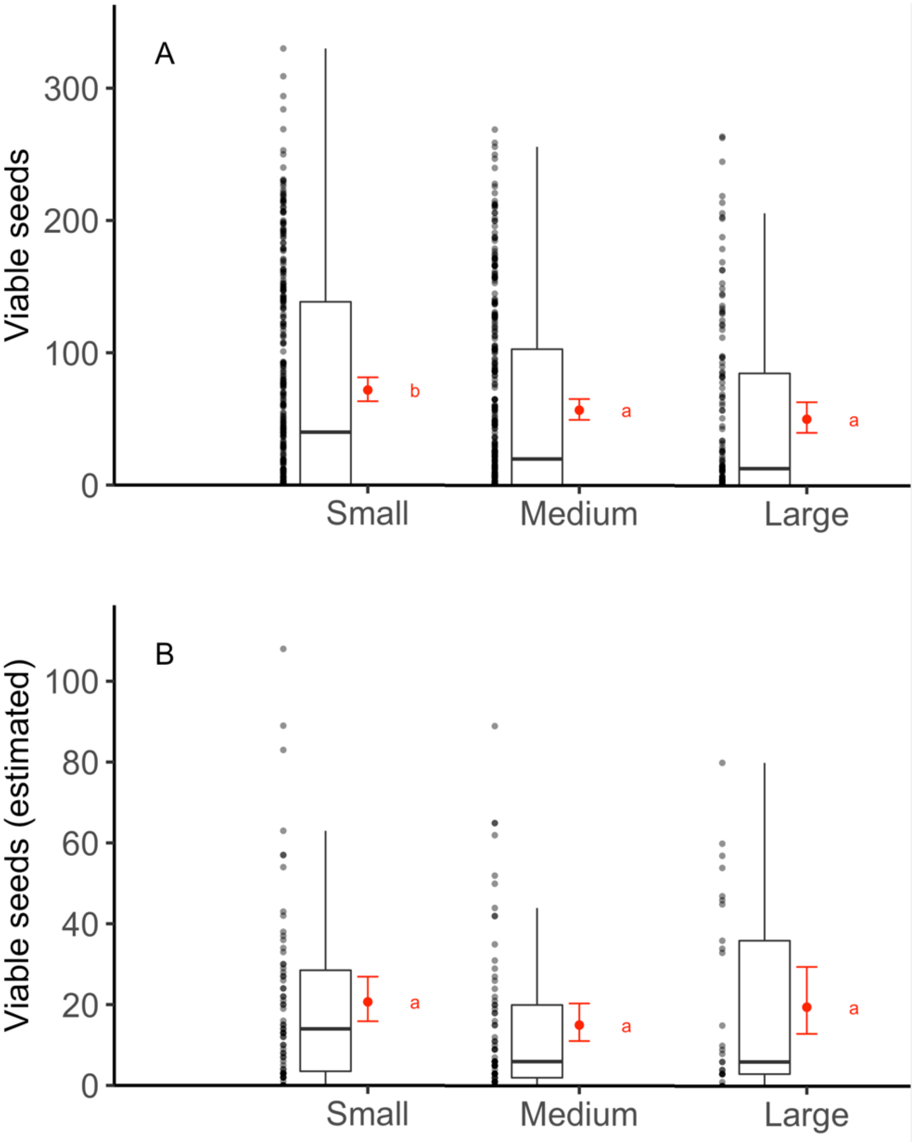


Figure 5.3: Boxplots showing the difference in viable seeds (estimated for *P. neriifolia*) between patch size categories, *E. discolor* (A) and *P. neriifolia* (B).

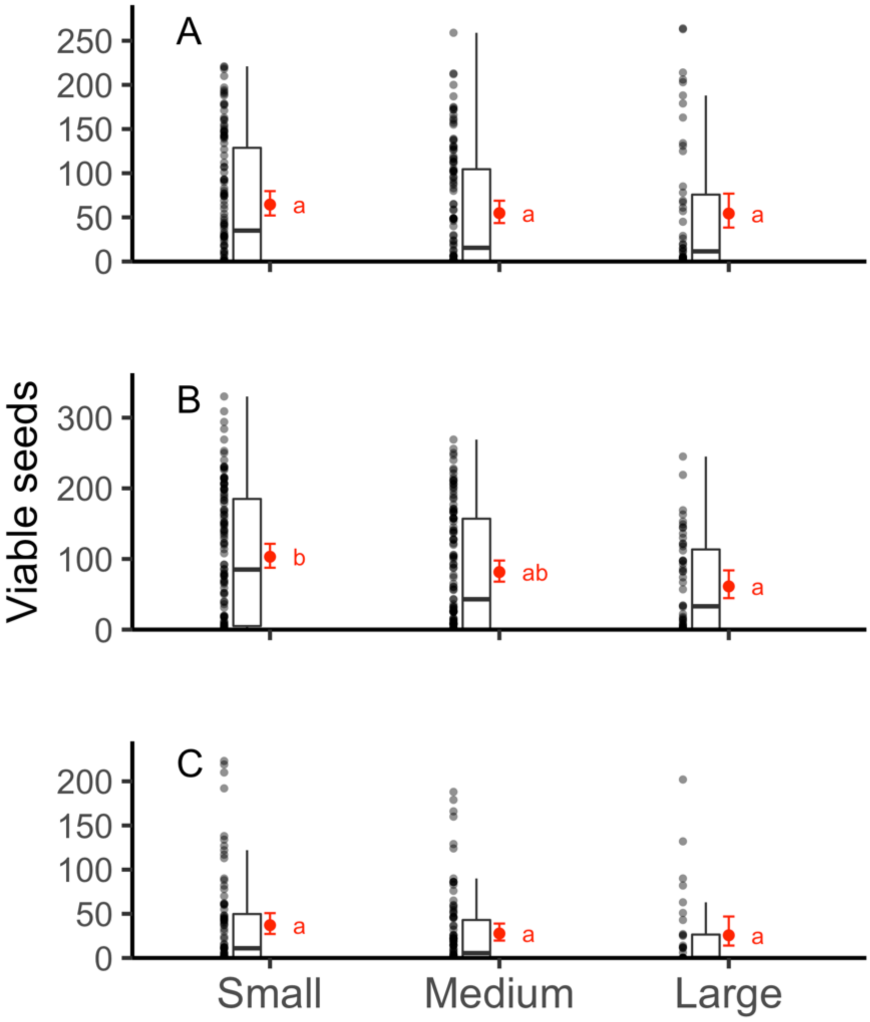


Figure 5.4: Boxplots showing the difference in *E. discolor* viable seeds between patch size categories for survey periods 4WI (A), 6SP (B), 8SU (C).

Table 5.1: Generalised linear model findings for *E. discolor* viable seeds and *P. neriifolia* viable seeds (estimated) with patch size.

Species	**Model**	**Term**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Erica discolor	Linear	Intercept	4.54	0.17	26.45	**<0.001**
		Patch size (log10)	-0.11	0.044	-2.52	**0.024**
	Segmented	Intercept	4.79	0.26	18.21	**<0.001**
		Patch size (log10)	-0.19	0.084	-2.31	**0.038**
		Patch size (log) U.1	0.28	0.21	1.31	0.21
Protea neriifolia	Linear	Intercept	2.88	0.32	8.94	**<0.001**
		Patch size (log10)	0.0012	0.079	0.015	0.99

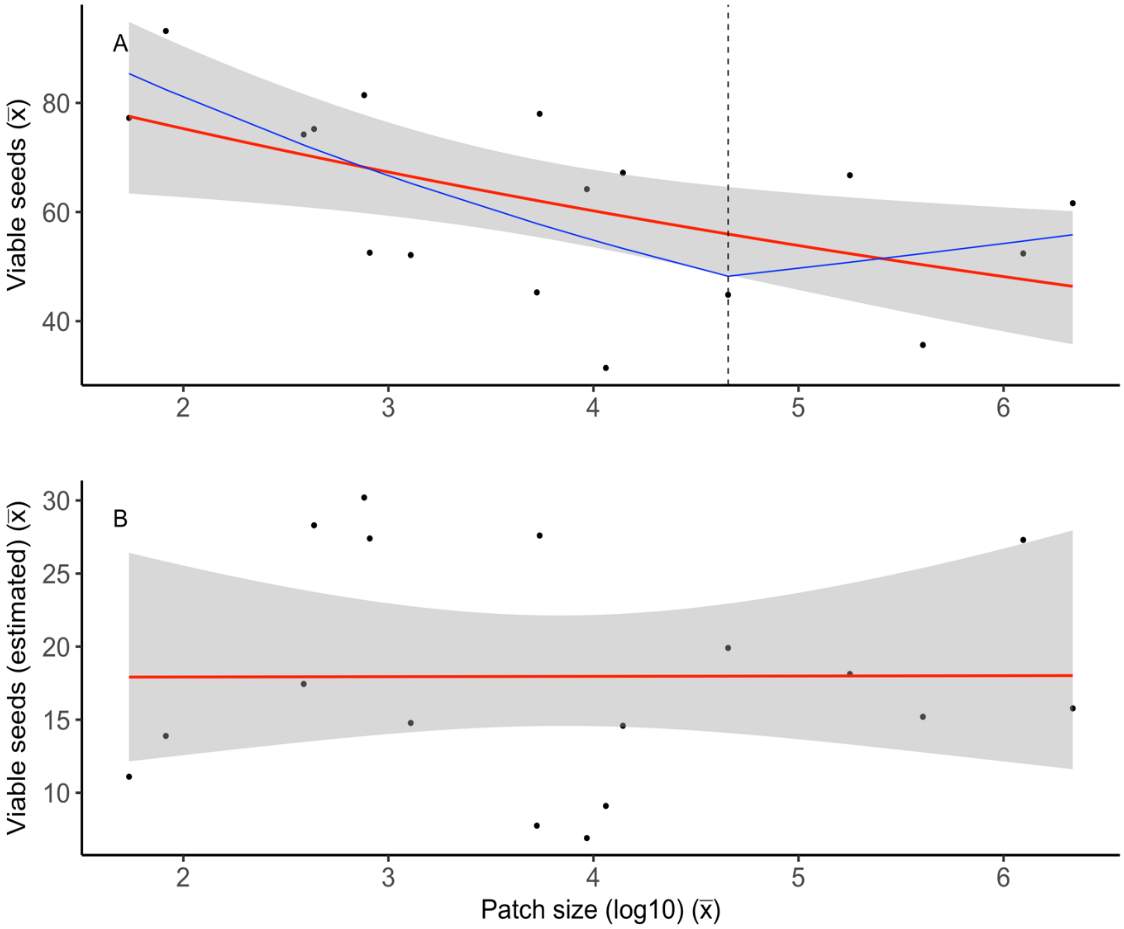


Figure 5.5: The relationships between mean viable *E. discolor* seeds (A) and mean viable *P. neriifolia* seeds (estimated) (B) with mean patch size (log10). The blue line on A is the segmented analysis estimate for the break (dashed line). Grey shading represents the 95% confidence intervals.

Seed-set compared with bird abundance

Southern Double-collared Sunbird abundance showed a non-significant positive relationship with viable *E. discolor* seeds whilst Orange-breasted Sunbird abundance showed a significant negative relationship (Table 5.2; Figure 5.6). Cape Sugarbird abundance showed no relationship with viable *P. neriifolia* seeds (estimated) (Table 5.2; Figure 5.7).

Table 5.2: Generalised linear model results for the relationships between *E. discolor* viable seeds and mean Southern Double-collared and Orange-breasted Sunbird abundance and *P. neriifolia* viable seeds (weighted) and mean Cape Sugarbird abundance.

Species	Term	Estimate	Std. Error	t value	Pr(> |t|)
Erica discolor	Intercept	3.86	0.19	20.16	**<0.001**
	Southern Double-collared Sunbird	0.11	0.072	1.53	0.15
	Intercept	4.34	0.1	41.66	**<0.001**
	Orange-breasted Sunbird	-0.14	0.057	-2.43	**0.028**
Protea neriifolia	Intercept	2.79	0.19	14.61	**<0.001**
	Cape Sugarbird	0.035	0.056	0.62	0.55

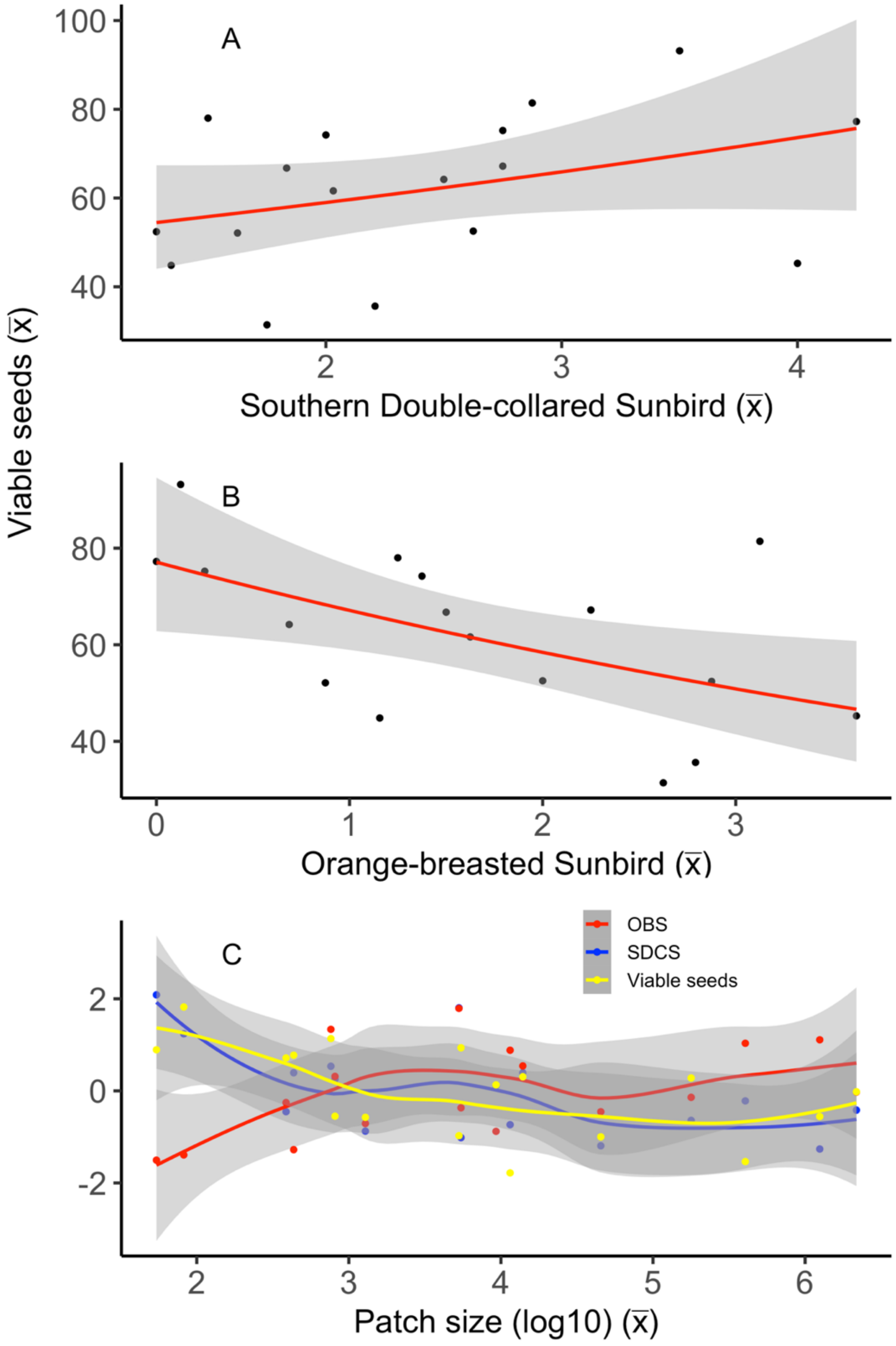


Figure 5.6: The relationships between mean abundance of Southern Double-collared (A) and mean abundance of Orange-breasted Sunbirds (B) and viable *E. discolor* seeds. The scaled relationships with patch size ($\log_{10}$) of mean Southern Double-collared Sunbird abundance (SDC), mean Orange-breasted Sunbird abundance (OBS) and viable E. discolor seeds are also shown (C). Grey shading represents the 95% confidence intervals.

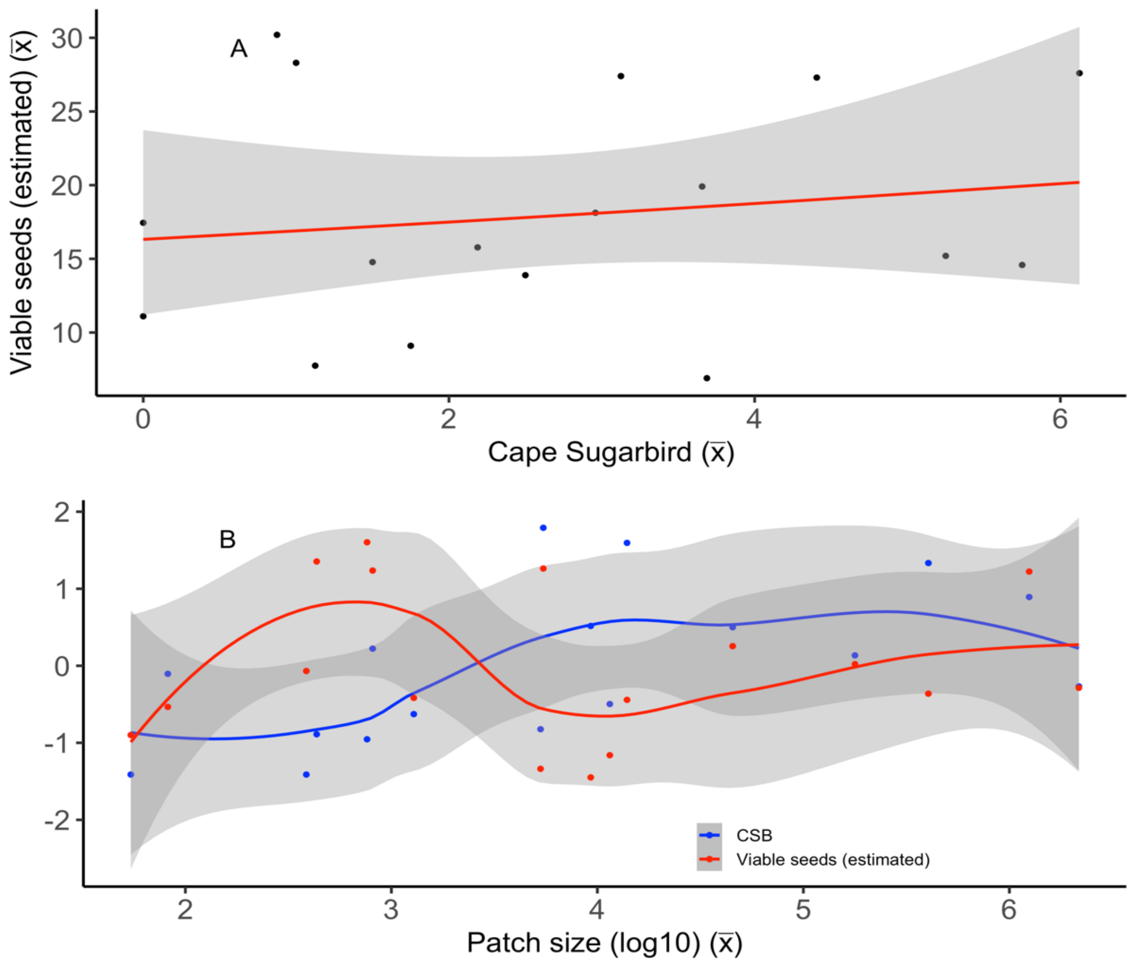


Figure 5.7: The relationship between mean Cape Sugarbird abundance and viable *P. neriifolia* seeds (weighted) (A). The scaled relationships with patch size (logged) of mean Cape Sugarbird abundance (CSB) and viable P. *neriifolia* seeds (weighted) are also shown (B). Grey shading represents the 95% confidence intervals.

Seed-set in relation to nectar volume

No significant relationships were found between *E. discolor* seed set and erica nectar or erica nectar availability, or between *P. neriifolia* seed set and protea nectar or protea nectar availability (Table 5.3; Appendix 5.2).

Table 5.3: Generalised linear model findings for mean *E. discolor* viable seeds with mean *E. discolor* nectar (and combined with biomass for potential erica nectar) and mean *P. neriifolia* viable seeds (weighted) with mean *P. neriifolia* nectar (and combined with protea density for potential protea nectar).

Species	**Term**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Erica discolor	Intercept	4.3	0.16	26.33	**<0.001**
	Erica nectar	-0.064	0.054	-1.17	0.26
	(Intercept)	4.14	0.11	36.92	**<0.001**
	Potential erica nectar	-0.00027	0.0013	-0.21	0.83
Protea neriifolia	(Intercept)	3.097	0.28	11.01	**<0.001**
	Protea nectar	-0.14	0.18	-0.79	0.44
	(Intercept)	17.43	2.76	6.32	**<0.001**
	Potential protea nectar	0.0031	0.012	0.27	0.79

Discussion

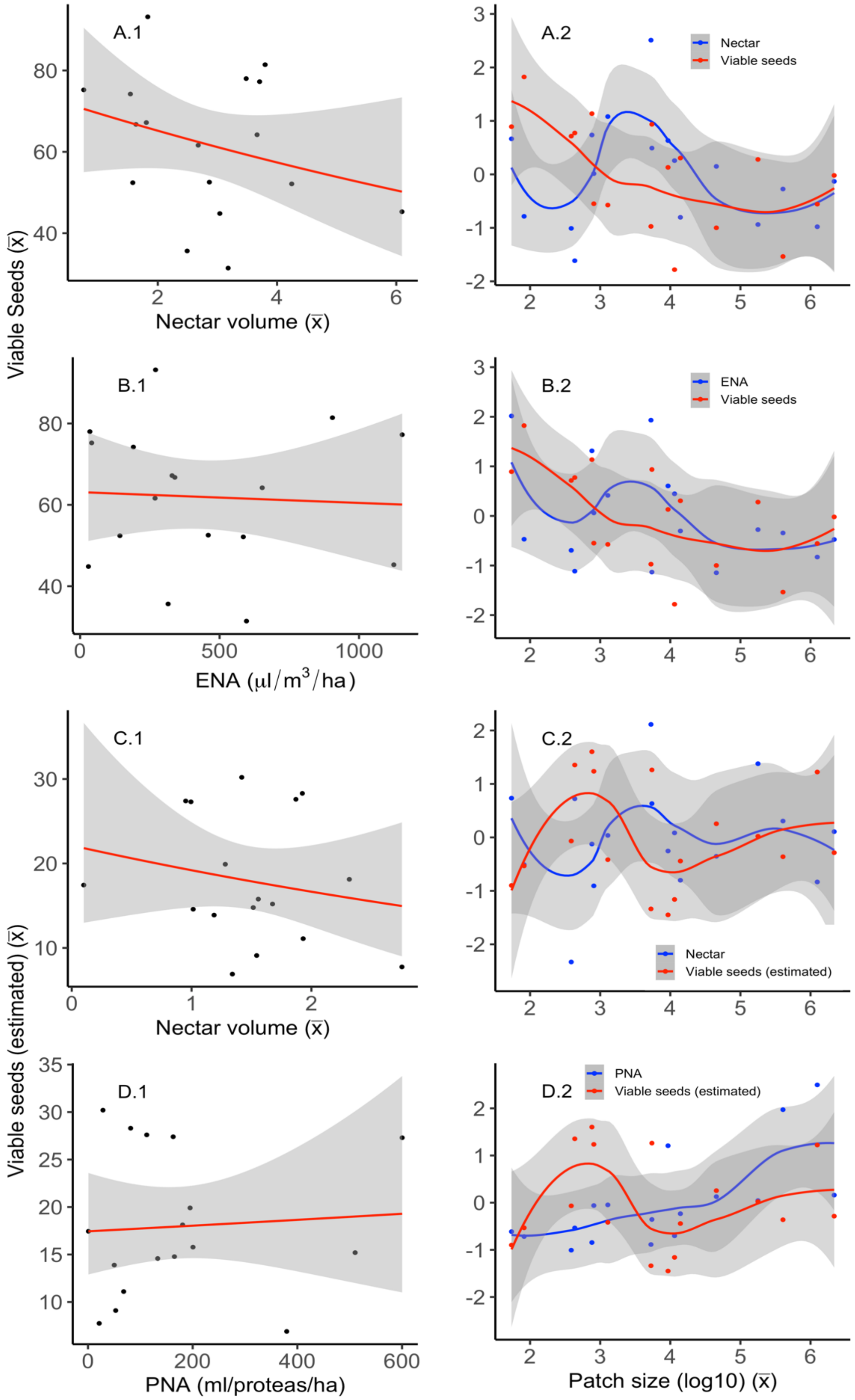
The findings of this investigation shows that habitat fragmentation can affect seed-set of the species considered. There are though many factors at play and the results vary based on the characteristics and ecology of the bird and plant species investigated. For *E. discolor* seed-set, the impact of fragmentation was overall positive as the plant species was exposed to additional avian pollinators from the surrounding matrix. As discussed in previous chapters, *E. discolor* is fed on and pollinated by both the fynbos endemic Orange-breasted Sunbird as well as the generalist Southern Double-collared Sunbird (Turner 2012; Angoh et al. 2021). *Erica discolor* seed-set was lower in large patches, which reflects that the species benefitted from the conditions in and around small patches and the higher abundance of Southern Double-collared Sunbirds (Angoh et al. 2021). In the large patches, Orange-breasted Sunbird was in higher abundance, and Southern Double-collared in lower, as shown in Chapter 3, but numerous factors likely contributed to the fact that *E. discolor* seed-set was lower. These factors may have included that Orange-breasted Sunbird had access to additional nectar resources including proteas, bulbs and other erica species, and that *E. discolor* were covered and displaced by more developed and mature overstory shrubs including protea, leucadendron and metalasia species (Geerts et al. 2020). *Protea neriifolia* seed-set, on the other hand, showed no relationship with patch size. This was likely more a reflection of the Cape Sugarbird's high mobility and ability to seek out isolated nectar sources, although they were more abundant in large sites as discussed in previous chapters. The results for both plant species should not be considered as evidence that habitat fragmentation cannot have a negative effect on pollination efficiency and seed-set. Geerts (2016), for example, showed in a study in the southwestern Cape of the CFR that habitat fragmentation is negative for the bird pollinated *Chasmanthe floribunda.* He found that the specialist pollinator for the long-tubed flowers, the long-billed Malachite Sunbird (*Nectarinia famosa*), was missing from the smaller transformed and fragmented sites (Geerts 2016). The short-billed Sunbirds present in these smaller sites, Orange-breasted and Southern Double-collared, were found to only rob nectar and not pollinate the plants as seed-set was significantly lower than the larger natural sites (Geerts 2016).

The findings on seed-set of these two species alone can thus not be used to motivate that there was a negative effect of habitat fragmentation in this study system. There were though several other bird-pollinated species that would likely have presented differently, including bulbs, leucospermum and other protea and erica species, that I could not investigate as they were not present in all the sites or occurred in low abundance and sporadically. Until further investigation is possible, and along with the findings from other chapters, the assumption should be that habitat fragmentation has a negative effect in the study system. All care should be taken by conservationists and managers to protect existing fynbos patches and to expand on it where possible.

Appendices

Appendix 5.1: Sample size, mean (with standard deviation) and median (with interquartile range) for viable seeds for small-, medium- and large-size patch categories for both *E. discolor* and *P. neriifolia*.

Species	Year/Survey period	Size category	N	Mean	SD	Median	IQR
Erica discolor	Year	small	307	71.84	80.69	40	138.5 (0 - 138.5)
		medium	321	56.9	71.4	20	103 (0 - 103)
		large	133	50.32	68.16	13	85 (0 - 85)
	4WI	small	112	64.48	70.49	35	128.75 (0 - 128.5)
		medium	114	54.77	66.57	15.5	104.5 (0 - 104.5)
		large	50	54.34	78.26	11.5	75.75 (0 - 75.75)
	6SP	small	115	103.14	93.12	85	180 (5 - 185)
		medium	117	81.46	83.78	43	156 (1 - 157)
		large	52	61.15	66.23	33	112.5 (1 - 113.5)
	8SU	small	80	37.14	54.82	11	49.75 (0 - 49.75)
		medium	90	27.68	43.46	5.5	43 (0 - 43)
		large	31	25.68	46.08	0	26.5 (0 - 26.5)
Protea neriifolia	Year	small	67	20.67	22.37	14	25 (3.5 - 28.5)
		medium	69	15.03	19.15	6	18 (2 - 20)
		large	29	19.55	23.59	6	33 (3 - 36)



Appendix 5.2: The relationships between mean *E. discolor* viable seeds with mean *E. discolor* nectar volume (A.1) and erica nectar availability (ENA - nectar combined with erica biomass) (B.1) and mean viable *P. neriifolia* seeds (estimated) with *P. neriifolia* (C.1) nectar volume and protea nectar availability (PNA - nectar combined with protea density) (D.1). The scaled relationships with patch size (log10) of mean *E. discolor* nectar volume and mean *E. discolor* viable seeds (A.2) as well as erica nectar availability (B.2) and of mean *P. neriifolia* nectar volume and mean viable *P. neriifolia* seeds (estimated) (C.2) as well as protea nectar availability (D.2) are also shown. Grey shading represents the 95% confidence intervals.

Chapter 6: Synthesis and conclusions

The aim of this study was to determine if habitat fragmentation had an impact on selected nectarivore birds and the fynbos plants that they pollinate in the seldom studied eastern Cape Floristic Region (CFR). I identified 17 fynbos patches where I conducted a year's fieldwork and collected data on bird species richness, abundance and seasonality, flowering phenology, nectar production and seed-set. In **Chapter 1** I introduced the study and the thesis topic of habitat loss and fragmentation in a general sense and then specifically in the context of bird pollination and the Cape Floristic Region. In **Chapter 2** I described my study area and how I selected and delineated my study patches. I used a Principal Components Analysis of the patch-selection criteria, as well as fragmentation and focal plant species variables to explore the fragmentation focus of study. This revealed that there is a discernable fragmentation pattern in the study that ranged from the intact fynbos and natural habitat surroundings in the large patches through to more impacted fynbos surrounded by transformed habitats in the small patches. This finding confirmed the premise of the study that follows on regional and global habitat loss and fragmentation research. For example, a study focusing on spider diversity in remnant fynbos patches in the western CFR found that both patch size and the amount of remaining habitat had a positive influence on spider diversity (Theron et al. 2020). A large cross-taxa study of forest-dependent species across the Brazilian Atlantic Forest biodiversity hotspot also showed that not only habitat loss, but also habitat fragmentation, both mediated by edge effects, had negative impacts on animal and plant species richness (Püttker et al. 2020).

In **Chapter 3**, I addressed bird species richness in and around the study patches, paying particular attention to nectar feeding birds; the fynbos endemic Cape Sugarbird (*Promerops cafer*) and Orange-breasted Sunbird (*Anthobaphes violacea*), and the habitat generalist Greater Double-collared (*Cinnyris afer*), Southern Double-collared (*Cinnyris chalybeus*), Amethyst (*Chalcomitra amethystina*) and Malachite Sunbirds (*Nectarinia famosa*). The surrounding non-fynbos habitat matrix had an impact on especially the small patches by exposing them to species not typically found in fynbos, as indicated by the greater species richness and faster species accumulation rate in small patches, compared with the medium and large patches. A study of a fragmented Southern Mistbelt Forest, South Africa, also showed that the type and quality of the surrounding non-habitat matrix had a strong positive influence on bird species diversity (Ngcobo et al. 2022). My findings also showed a clear habitat fragmentation effect on nectar feeding birds, but this strongly depended on the species characteristics and habitat and dietary preferences. The fynbos endemic, Orange-breasted Sunbird was scarce or absent from small patches. The habitat generalist Southern Double-collared Sunbird, its closest competitor in terms of size and bill-length, as well as the larger Greater Double-collared and

Amethyst Sunbirds, were in contrast abundant in small patches. These generalist species utilise and benefit from the habitat and resources in most of the non-fynbos habitat matrix surrounding the fynbos patches. The fynbos endemic Cape Sugarbirds, along with Malachite Sunbirds, were also lower in abundance in the smallest patches that were also found to have the lowest protea densities. Both Cape Sugarbird (fynbos) and Malachite Sunbird (not just fynbos) seems to prefer larger, less impacted habitats with higher resource availability for feeding (insects and nectar) and nesting (Daniels et al. 2001; Symes et al. 2001; Potgieter et al. 2008; Schmid et al. 2016). A study in the Rogue Basin, Oregon, USA using a species-centered model (in contrast to a land-cover model), also revealed a strong effect of fragmentation on bird species richness (Halstead et al. 2019).

In **Chapter 4**, I investigated the influence of patch size on flower nectar loads and overall nectar availability of the most abundant erica and protea species in the study area. Neither *Erica discolor* nor *Protea neriifolia* nectar loads showed a clear response to patch size, but erica nectar availability per unit area decreased as patch size increased, whilst protea nectar availability increased. I also considered how the nectarivore birds related to the plant species on which they feed, with Southern Double-collared Sunbird and Cape Sugarbird abundance increasing with erica and protea nectar availability, respectively and Orange-breasted Sunbirds not showing a pattern. It appears that bird abundance and nectar availability did not necessarily have a direct causal relationship. The conditions for proteas to grow more densely and abundantly in larger patches resulted by default in higher nectar availability, with the same true for the ericas in small patches. Bird relationships with nectar availability were thus confounded by their preferences for fynbos habitat and plant structure, rather than just nectar availability per se. In a study that only considered Proteaceae nectar (not erica), nectar feeding bird abundance and richness was most strongly correlated to nectar availability rather than vegetation structure or plant community composition (Geerts et al. 2020). However, the results from Geerts et al. (2020) are not directly comparable because their small 1 ha fynbos plots were in non-fragmented areas, and differed considerably in terms of vegetation age, with many of the plots burned within the last four years. Their study confirms the findings of other studies that have shown that Cape Sugarbirds are seldom present in fynbos vegetation older than four years of age (Geerts et al. 2012, 2020). My study thus confirmed a relationship between nectar and nectar feeding bird abundance, but I was not able to draw further conclusions concerning fynbos habitat preference and structure. I also considered the seasonality of protea flowers, their nectar production, and Cape Sugarbird presence and abundance for the study area, and found they were all positively related and peaked in summer. These findings corresponds with studies from the all-year rainfall eastern CFR but contrasts with the winter rainfall western CFR where protea flowering peak in winter (Heelemann et al. 2008; Carlson et al. 2011; Kraaij et al. 2013b). Cape Sugarbirds track nectar seasonally and over large distances (e.g. a ringed bird travelled 160 km) (Fraser et al. 1989; Altwegg & Underhill 2006; Whitehead 2018). It is thus reasonable to assume that Cape Sugarbirds move seasonally between the eastern and western CFR although there are no studies that have specifically looked at it.

In **Chapter 5**, I considered seed-set of the selected fynbos plant species across the study patches. *Protea neriifolia* seed-set showed no defined pattern, which is likely a reflection of the high mobility of Cape Sugarbirds, but it could also just be that I did not have a large enough sample size to reveal a pattern. *Erica discolor* seed-set showed a clear pattern with higher seed-set in the small patches. This related negatively to Orange-breasted Sunbird abundance but showed no relationship with Southern Double-collared Sunbirds. I suggest, like the findings with nectar availability, that the relationship was more a reflection of the Orange-breasted Sunbird's preference for fynbos habitat rather than their role as pollinator. However, Southern Double-collared Sunbirds can pollinate *E. discolor* in the absence of Orange-breasted Sunbirds. These results confirm the findings of a similar study conducted in the area. Using anther ring disturbance as a proxy for flower visitation, the study showed no difference in visitation rates to *E. discolor* among fragmented patches, and also found higher seed-set in small patches (Angoh et al. 2021).

My results suggest that habitat fragmentation is not a major concern for the persistence of the bird pollinated plant species included in the study. This conclusion is supported by the findings of a global synthesis on the impact of fragmentation of plant progeny quality (Aguilar et al. 2019). The synthesis found that insect- and wind-pollinated plants tended to have reduced germination, survival and growth, and overall genetic erosion in fragmented habitats, whereas plants pollinated by bats and birds were generally not as negatively affected, likely because their pollinators are better able to move between fragments (Aguilar et al. 2019). A study in the eastern CFR that considered the impact of different land-cover types (intact fynbos, alien vegetation thicket, and pastures/rangelands) on the pollination of bird-pollinated *Erica glandulosa* in road-verges also showed that bird nectarivores still managed to visit the flowers under all conditions, albeit sometimes with much reduced pollination rates (Grobler & Campbell 2022). However, the study did not test if the reduced pollination rates in especially the road-verges next to the pastures/rangelands was sufficient to maintain populations of the seed-dependent plant species (Grobler & Campbell 2022). It is important to remember though, that the effects of habitat fragmentation vary between species, the type and combination of organisms, the aspects being investigated, the populations studied, the spatial and temporal scales of the study and where in the world the study is taking place (Banks-Leite et al. 2020). For instance, the natural fire disturbance history of the fynbos system has likely shaped the sensitivity of local species to fragmentation with only potentially less sensitive species remaining (Betts et al. 2019). Because of all the variables at play and although some strong findings can be drawn from the study, we should be cautious not to draw too broad conclusions from this study.

Study limitations and future research

I was able to show strong and useful results within the confines of the study design and chosen study area. However, there were important ecological and conservation related questions that I could not address, notably the effect of time since fire as well as the impact of alien vegetation (Kraaij et al. 2013a, 2013b; Baard & Kraaij 2014). Most of the study area was burned in one large regional fire in 1998 (Kraaij et al. 2013a). Although some fires have occurred since then, none have impacted the study patches I had available for selection. All the potential patches in the study were also either already clear, or mostly cleared of alien invasive vegetation through the Garden Route National Park (GRNP) alien-clearing programmes (M. Alant, SANParks, pers. comm.). The removal of these confounding variables (time since last fire and alien invasive vegetation infestation levels) allowed for a deeper focus on just habitat fragmentation and the surrounding non-habitat matrix, and clearer interpretation of the findings. However, I could not draw conclusions and make management and conservation recommendation that consider these important factors. This is especially relevant as I only ended up including 17 study patches rather than the 30+ sites that I originally planned for. I had to exclude several patches as they did not meet the criteria that would have allowed for comparison. I also expected to have more plant species to study, but in the end only had four, and only two widespread and abundant species that could be compared among patches. A wider selection of plant species would potentially have revealed more defined fragmentation patterns and might also have included species that could have been more negatively impacted by the absence of their specialist pollinators in small patches (Geerts 2016). Where my study focused on abundant and widely occurring plant species in the area, I suggest for future research that species should also be targeted based on their local extinction risk (Cowell et al. 2022). This will require the identification of such species through field surveys, of which organisations such as the Nature’s Valley Trust and South African National Parks have done. Focusing on abundant and widely occurring species can inform broad conservation and management action. Conversely, focusing on species based on their local extinction risk inform and prioritise immediate and targeted management action such as path closure, habitat rehabilitation and alien invasive plant clearing (Cowell et al. 2022). A further consequence of the smaller selection of study patches, along with the fact that the selection ended up quite grouped, is that patch size was correlated with available fynbos habitat around a patch. I could thus not determine if Island Biography Theory or the Habitat Amount Hypothesis had more explanatory power for the impact of habitat fragmentation in the study system. I would thus suggest for future research that the selection criteria are defined as early as possible in the project so the study area can be increased if it turns out that there are too few comparable patches after field visits.

Conclusions and management recommendations

The findings of the study clearly show that habitat fragmentation has an effect in the study system, although this could be negative or positive depending on what study aspects and plant and bird species were considered. If I consider the findings as a whole, I'm able to define a trend. There appears to be a tradeoff between protea and erica density as you go from small patches (more ericas/less proteas) to large patches (less ericas/more proteas). This tradeoff is broadly reflected in each patch through the nectar availability, the nectarivore bird balance, and in the seed-set. For example, fewer proteas in small patches means more ericas and higher erica nectar availability, which means fewer Cape Sugarbird and Malachite Sunbirds, but also more Southern and Greater Double-collared and Amethyst Sunbirds that spill over from the surrounding matrix that result in higher erica seed-set.

I was pleasantly surprised by the overall positive finding that the main plant species studied, *P. neriifolia* and *E. discolor*, were able to persist and even thrive in the small patches (with the proviso that the present patch conditions are maintained, such as low alien vegetation infestation levels and an appropriate fire regime). However, it is important to note that for *P. neriifolia* there will likely be thresholds of, for example, patch isolation, size, alien vegetation infestation and fire-regime disturbance, which I could not define, where they will no longer persist. Similarly, Orange-breasted Sunbirds will also likely cease to occur below certain thresholds. However, it is important that small and isolated habitat patches should not just be discarded as not being important for biodiversity conservation. A global synthesis found that small habitat patches are often inordinately important for biodiversity conservation (Wintle et al. 2019). Care should thus be taken to ensure that any remaining habitat patches, irrespective of their size and isolation, are considered for conservation and management action.

Conservation and management authorities should aim to conserve and expand on remaining fynbos habitat by; keeping it clean of and clearing the surrounding non-habitat matrix of invasive alien vegetation, rehabilitation and restoration of land that might become available after, for example, cessation of commercial forestry, and to maintain appropriate fire regimes. Through this, the species covered in the study, as well as potentially more sensitive and less abundant species, will be able to persist. South Africa has a long-term plan in place for invasive vegetation management and eradication, Working for Water (van Wilgen & Wannenburgh 2016). This programme was initiated as a poverty relief programme and to assist both state-owned organisations and private landowners to control and eradicate alien vegetation to sustain water yields from catchment areas (van Wilgen & Wannenburgh 2016). Although the programme has had considerable success, no species have been successfully controlled or any areas permanently cleared (van Wilgen et al. 2022). Invasive vegetation is among the largest threats to fynbos vegetation and ecosystems and urgent long-term focussed action is required (Baard et al. 2017). The study area has had good working relationships between the GRNP and public landowners through the Redford and Southern-Crags conservancies on conservation management issues, including invasive vegetation control (SANParks 2020). All the study patches included in the study were reasonably cleared of alien invasive species prior to the study commencing (M. Alant, SANParks pers. comm.). Some researchers suggest that as long as previously disturbed fynbos areas are kept clear of alien invasive vegetation, and there is sufficient nearby native vegetation, then active restoration is most likely unnecessary (Boxriker et al. 2022). If, for example, a cleared exotic tree plantation or an area heavily infested by alien vegetation is restored, then active restoration i.e. soil restoration treatment and sowing native seeds may be more beneficial than passive restoration, but not necessarily so (Hall et al. 2021; Froeschlin et al. 2022). There is a good chance that with the present policies and programmes in place, that the patches in the study area will remain largely clear of infestation. However, the larger concern is whether the largely inaccessible intact areas of fynbos can be kept clear (Baard et al. 2017). National surveys indicate that plant invasions have continued to grow despite control efforts to date (Henderson & Wilson 2017). The proposed solution, including for the study area, is that clearly defined priority sites should be targeted such as water supply catchment areas, that appropriate and cost-effective solutions should be implemented, and that the operations should be planned for long-term monitoring and follow-up (de Lange et al. 2022; van Wilgen et al. 2022). A successful example in the area is the clearing of the Keurbooms River catchment of alien invasive vegetation from 2015 to 2017 (Booth 2017). Funding was sourced privately via the Table Mountain Fund and others, and after the completion of the programme, there was a marked improvement in water supply to the town of Plettenberg Bay (Booth 2017). The harsh reality is that it is not realistic to expect that control can be achieved everywhere but in the study area there is enough motivation and resources by parties involved to hopefully clear and maintain key areas.

A further complication regarding fynbos in a fragmented and human populated landscape with alien invasive vegetation spread, is the management and implementation of appropriate fire regimes (Driscoll et al. 2021). To maintain fynbos health in the broader study area, fynbos should burn approximately every 15 years (Kraaij et al. 2013b, 2020; Kraaij &

van Wilgen 2013). As it stands, most of the fynbos in the study area was burned over 25 years ago (Kraaij et al. 2013a). As a result, much of the fynbos, especially in the large intact patches, is becoming senescent and starting to be invaded by forest precursor species. The GRNP management plan makes provision to follow the recommended fire regimes (SANParks 2020), but this is not implemented because of the fear of runaway fires and resultant property damage. Private and public owners of the small patches in the study, are also reluctant to burn for the same reasons. The threat is exacerbated by the high invasive alien vegetation loads surrounding many of the patches which increases the risk of high intensity fires (Msweli et al. 2020; Kraaij et al. 2022). The consequences of such uncontrolled fires were demonstrated with the devastating regional fire between George and Plettenberg Bay in 2017 when 15 000 ha burned, destroying 800 houses and killing seven people (Kraaij et al. 2018). However, it is important for the fynbos in the area to burn. The GRNP and other owners of fynbos patches must work together with the local environmental organisations and fire protection agencies to develop a coordinated fire plan. If it does not burn soon, the fynbos will just continue to densify, become woodier and increase the risk of uncontrolled fire. It is also important after managed fires, that the GRNP and other involved organisations should follow up and intensify their alien invasive vegetation clearing programmes. Shortly after fire is practically the best time to clear alien vegetation but the best results will follow a comprehensive pre-/post-fire clearing and reseeding programme (van Wilgen 2009; Holmes et al. 2020).

The study area has many positives going for it regarding the maintenance and even expansion of the present fynbos (and other natural) areas. If alien invasive plant clearing efforts and fire regimes are maintained, the fynbos vegetation and associated plant and animal species and ecosystems will persist. The GRNP encompasses the wider area and within that falls protected areas formally managed by Cape Nature Conservation, as well as more and more private land being set aside for conservation through stewardship agreements. Examples include the Robberg Coastal Corridor as well smaller private protected areas such as Brackenburn Private Nature Reserve. The area also has a strong set of environmental non-governmental organisations and conservancies such as the Nature's Valley Trust, Addo to Eden, Plettenberg Bay Community Environmental Form, the Garden Route Biosphere Reserve, and the Redford and Southern Crags Conservancies. Such organisations have strong conservation values and are capable of running projects that have positive conservation outcomes (Botha 2020; Jubase et al. 2021). All these organisations have a common goal to protect the environmental integrity of the area, and to prevent further habitat loss and degradation, arguably the most important step to reduce the impacts of habitat transformation (Banks-Leite et al. 2020).

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